Seasonal changes in biomass, elongation growth and primary production rate of *Chara tomentosa* in the NE Baltic Sea

Kaire Torn\(^1,2\), Georg Martin\(^1\) & Tiina Paalme\(^1\)

\(^1\) Estonian Marine Institute, University of Tartu, Mäealuse 10a, 12618 Tallinn, Estonia (e-mail: kaire.torn@ut.ee)
\(^2\) Institute of Botany and Ecology, University of Tartu, Lai 40, 51005 Tartu, Estonia

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The seasonal dynamics of the biomass, elongation growth and primary production rate of the green alga *Chara tomentosa* were measured in Rame Bay (NE Baltic Sea) during the vegetation period of 2002. The measurements showed extremely high plant height (up to 142 cm) and biomass values (5.2 kg\((\text{w.w.})\) m\(^{-2}\)), indicating the importance of *C. tomentosa* for the whole coastal water ecosystem. The apical part of the thallus grew more intensively from early spring to midsummer. The growth rate of the subapical section was very low during the entire observation period. The plant’s diurnal net primary production rate peaked in July (43.4 mg\(\text{O g(d.w.)}^{-1} \text{24h}^{-1}\)); remarkably lower rates were measured in May and September. The elongation growth and primary production were not correlated with water nutrient concentrations and water temperature. As the active growth of *C. tomentosa* takes place during a relatively short period at the beginning of summer, the amount of available solar radiation and the temperature levels during this sensitive time can have a significant effect on the community in the same year.

Key words: Baltic Sea, biomass, *Chara tomentosa*, elongation growth, primary production rate

Introduction

The green alga *Chara tomentosa* is found in fresh waters all over the globe. In brackish waters *C. tomentosa* only occurs in the Baltic Sea (Björkman 1947, Torn *et al.* 2003). The species can be encountered in all coastal areas of the Baltic, yet tends to favour the northern part of the sea (Pankow *et al.* 1990, Nielsen *et al.* 1995, Torn *et al.* 2003).

*Chara tomentosa* is among the largest charophyte species in the Baltic Sea. In favourable conditions the plant can attain a height of over 30 cm. Despite its sturdy appearance the species has a fragile thallus and thus usually prefers sheltered areas with soft muddy or sandy bottoms. *Chara tomentosa* can hibernate as a full-grown plant and continue growth in the following spring from the nodes at the top (Olsen 1944, Corillion 1957, Lundegårdh-Ericson 1972). This
manner of hibernation allows the species to recommence growth promptly after break-up of ice (Munsterhjelm 1997).

*Chara tomentosa* may occur together with other charophytes or with vascular plants, but primarily forms dense monospecific stands (Torn *et al.* 2003). These communities have been suggested to be of considerable ecological importance in regulating water quality by binding nutrients and by being an important habitat for invertebrates and ichthyofauna (Henricson 2002). *Chara tomentosa* is included in a Red Data Book of charophytes in the Baltic Sea (Blindow *et al.* 2003). During the second half of the 20th century the distribution of *C. tomentosa* decreased strongly in some areas of the Finnish Archipelago Sea and in the German coastal seas. Only relatively dated records regarding the distribution of the species along the Latvian and Lithuanian coasts exist (Koistinen & Munsterhjelm 2001, Torn *et al.* 2003). In Estonian waters *C. tomentosa* is at present restricted to western Estonia only, although the species has previously also been registered in the southern part of the Gulf of Finland. Shallow, closed and sheltered coastal lagoons are typical habitats for the species in the West-Estonian Archipelago Sea. In the Estonian coastal seas, high-biomass monospecific *C. tomentosa* communities have been found in at least three locations, including Rame Bay (Torn *et al.* 2004).

As compared with other aquatic plants, there have been fewer studies of the ecology of charophytes, especially in brackish conditions (Coops 2002, Schubert & Blindow 2003). There are few estimates of charophyte growth rates covering the species’ entire growth cycle (Best 1981, Blindow *et al.* 1998, Fernández-Aláez *et al.* 2002). Moreover, the studies yielding the estimates were conducted predominantly in freshwater environments and focused exclusively on biomass estimation. So far only laboratory studies regarding the elongation growth of charophyte species in brackish conditions have been carried out (Henricson 2002, Blindow *et al.* 2003). The data concerning the photosynthetic activity of *C. tomentosa* in brackish water are scarce (Libbert & Walter 1985, Ritzl 2000, Kotta *et al.* 2004).

The aim of the present study was to fill the gap in the knowledge about the biology of *C. tomentosa* by describing the seasonal variation of the biomass and elongation growth and evaluating the primary production rate of the species.

**Material and methods**

**Study site**

Rame Bay, located in the northeastern Baltic Sea (Fig. 1), is a shallow and semi-enclosed sea inlet on the western coast of the Estonian mainland. The bay receives its waters from the West-Estonian Archipelago Sea characterised by features typical of a frontal zone between the eutrophic waters of the Gulf of Riga and the less eutrophic waters of the northern Baltic proper (Suursaar *et al.* 1998). The maximum depth of the area is 1.5 m but most of the bay is shallower than 1 m. The bottom is composed of fine sand and a thick layer of silt. Salinity varies between 3–5 PSU largely in accordance with rainfall.

As a sheltered body of water, Rame Bay provides an excellent habitat for luxurious charophyte populations together with aquatic phanerogams. Previous investigations have reported coverage rates of phytobenthos communities ranging from 15% to 100% (Torn & Martin
Four species of charophytes were identified in the bay. A *Chara aspera* community was observed in shallower areas while *C. tomentosa* formed dense stands in somewhat deeper areas in the northern part of the bay. Eleven percent of the total area of Rame Bay was covered by a *C. tomentosa* community with 100% coverage. Occasional *C. canescens* plants were found inside the *C. aspera*-dominated community. *Chara baltica* occurred as single specimens in a *Potamogeton pectinatus*-dominated community in the central and northern parts of the bay.

**Field measurements**

Quantitative samples of *C. tomentosa* communities were collected in May, July and September 2002. Unfortunately autumn measurements failed due to a malfunction of the freezer. Three replicates were collected using a 20 × 20 cm frame placed randomly inside the community. In the laboratory the species were determined and the biomasses of charophytes and other macroalgal species measured.

Field experiments were carried out from April to October at the depth of 1–1.2 m. Using SCUBA diving, growing plants were labelled and the first internode was marked in each plant. The lengths of the apical and the subapical sections were measured with a ruler. The apical section was defined as including the top of the plant until the base of the whorl directly above the marked internode. The subapical section was defined as including the marked internode together with the basal whorl (Fig. 2). The labelling was carried out on three separate occasions, in April, July and September, once each month. After each labelling, all marked plants were measured in the first, third and fifth weeks. Thus, the measured period for which growth could be assessed varied between 7 and 17 days. Altogether 30 replicate plants were measured in each series. However, the damage caused by the impact of waves and unforeseen mechanical disturbance reduced the number of measurable replicates from 5 to 26.

*In situ* measurements of diurnal primary production rate of *C. tomentosa* were carried out in May, July and September. In each month photosynthesis was measured during a period of 24 h. The same plant sections were used for elongation growth estimations. The net primary production (i.e. net photosynthetic) rates were measured using the oxygen method. Fragments of *C. tomentosa* without macroepiphytes and grazers were placed in 600 ml glass bottles, filled with seawater and incubated horizontally on special trays at 0.5 m depth. Bottles without algae served as controls. There were three replicates per treatment and three controls. For determination of the dark respiration rate the incubation bottles were wrapped in aluminium foil. Changes in dissolved oxygen concentration were measured using an oxygen sensor OXI 92 (WTW GmbH). The changes were then converted to percentage of dry weight increment by standard methods (Strickland & Parsons 1968) assuming a photosynthetic quotient of 1.2. The carbon content

![Fig. 2. Illustration of measurements. I = apical section, II = subapical section, A = internode label, B = plant number label.](image-url)
of algal tissue (TOC) was determined for each sampling period using the combustion catalytic oxidation/NDIR method.

During the production rate estimation experiments, water temperature (°C) was measured at incubation depth. Water nutrient concentrations were also measured during the experimental period. Replicate water samples were taken in May, July and September, once each month. The samples were analysed for phosphorus (PO$_3^-$ and total P) and nitrogen (NO$_2^-$ + NO$_3^-$ and total N) concentrations. Nutrient analyses were performed using standard colorimetric procedures with autoanalyser SKALAR.

**Results**

The height of the plants measured during the vegetation period of 2002 varied between 40 and 142 cm. In all cases most of the plant thallus laid on the seafloor, with only an apical part of 30–40 cm directed towards the surface. In most of the plants, decomposition on basal parts of the thallus was observed. The total mean biomass of the *C. tomentosa* community was (mean ± S.E.) 2.4 ± 0.311 kg(w.w.) m$^{-2}$ in May and 5.2 ± 0.847 kg(w.w.) m$^{-2}$ in July.

The elongation growth of the apical section of the plants was measured eight times during the investigation period (Fig. 3). The apical part of the thallus grew more intensively from the early spring to midsummer; growth declined somewhat in late July and August (the difference, however, was not statistically significant). The growth was significantly slower in September and October. The maximum elongation rates were 0.34 cm 24h$^{-1}$ in June and 0.31 cm 24h$^{-1}$ in July. As for the subapical section, despite somewhat higher values in May and August (around 0.06 cm 24h$^{-1}$), its growth rate remained very low during the entire observation period, with no seasonal differences observed.

The net production (photosynthetic) rates (NP) peaked in July (Fig. 4). The maximum NP rates (both for apical and subapical sections) varied between 4.1 and 5.3 mgO g(d.w.)$^{-1}$ h$^{-1}$, resulting in diurnal NP rates of up to 43.4 mgO g(d.w.)$^{-1}$ 24h$^{-1}$. Significantly lower NP rates were measured in May and September.

Seasonal changes in dark respiration (DR) rates followed the changes observed in NP rates. The highest DR rates (0.9 mgO g(d.w.)$^{-1}$ h$^{-1}$) were measured in July and the lowest (down to 0.2 mgO g(d.w.)$^{-1}$ h$^{-1}$) in September. There was a positive linear correlation between water temperature and DR rates ($r = 0.97$).

The elongation growth rates of the apical section were correlated with the net production rates calculated as the rate of diurnal oxygen evolution per dry weight as well as the percentage of algal dry weight increment in 24 hours (Fig. 5). High correlation ($r = 0.98$) was observed between measured growth rates and growth rates calculated from the diurnal primary production values.

Daytime water temperatures were exceptionally high in 2002, ranging from 11.4 to 16.7 °C in

![Fig. 3](image-url) Seasonal variation in average elongation growth + S.E. of *Chara tomentosa*. The date of measurement and the duration of the experimental period (in parentheses) are indicated. The number of replicates is indicated at the top of the bar.

![Fig. 4](image-url) Seasonal variation in average diurnal net primary production rate + S.E. of *Chara tomentosa*. In each period photosynthesis was measured in the period of 24 h replicated three times.
May, from 23.2 to 28.0 °C in July and from 12.3 to 13.8 °C in September. The dynamics of water nutrient concentrations during the observation period were different respectively for phosphorus and nitrogen compounds (Fig. 6). Nitrogen concentrations showed no clear trend during the study period while a rising trend was observed regarding phosphorus concentrations.

Discussion

Chara tomentosa found in Rame Bay represents a community with extremely high plant height and biomass values. The maximum height of C. tomentosa plants in the bay (142 cm) was twice higher than had been reported earlier (Torn et al. 2003). The mean biomass values of the community remained within the limits reported earlier by Trei (1965) in the same area (3.7–5.5 kg(w.w.) m⁻²). According to our data the community studied is one of the few high-biomass macrophyte communities found on soft substrate in the northern part of the Baltic Sea (Kautsky 1988, Martin 2000, Berglund et al. 2003). Thus, it is likely that Rame Bay provides optimal conditions for the development of C. tomentosa communities. Previous investigations show that the total area occupied and the total biomass of C. tomentosa community in the bay have practically not changed during the last 20 years, with only a slight shift observed in the exact location of the bay’s charophytes (Torn & Martin 2003). At the same time, a decrease of C. aspera and an increase of Potamogeton pectinatus stands have been recorded. Thus, the decrease of the proportion of charophytes in the benthic vegetation of Rame Bay from 74% in 1983 to 56% in 2002 was due to the decrease of C. aspera while the C. tomentosa community remained stable. A shift from charophyte-dominated communities to communities dominated by submerged phanerogams has been described for shallow-lake and brackish ecosystems as a response to eutrophication (Lang 1981, Moss 1989, Scheffer et al. 1992, Yousef et al. 1997). In the present study, the signs of increasing eutrophication were lacking but the general decrease in the importance of charophytes in coastal shallow ecosystems of NE Baltic Sea has been also explained by certain environmental factors e.g. the land uplift process (Munsterhjelm 2005).

It is known that charophytes grow in stable conditions apically and the elongation of the
apical cell stops after reaching a certain limit (Lee 1999). Our results confirmed this observation, since the apical sections measured during our study grew significantly faster than the subapical ones. It has been shown that the intermediate internodes are able to elongate in poor light in extremely turbid water (Hasslow 1931, Henricson 2002). In our study we did not find any extremely long internodes, which suggests an absence of extreme conditions in terms of light. A close examination of the morphology of *C. tomentosa* showed that the strategy of fast growth in the apical part of the thallus was accompanied by decaying processes in the basal part. Similar growth patterns have been found also in other charophyte species, for instance, in *Chara hispida* (Andrews *et al.* 1984). This mechanism helps the species to compensate for light deficit in dense stands. In extreme cases, the plant continues to grow even when the basal part of the thallus has fully decomposed. The apical internodes have also been reported to be capable of developing additional rhizoids for compensating decomposition in the basal part (Henricson 2002).

The seasonal dynamics of the elongation growth of *C. tomentosa* followed the general tendencies described for temperate-zone macrophytobenthos communities. The highest growth rates occur in the beginning of summer and a slowing down starts in August (e.g. Fernández-Aláez *et al.* 2002). Unlike these general patterns, the growth rates of the charophytes started to decline already in midsummer. The main growth in the biomass of the community is expected to take place during the first part of the vegetation period lasting until midsummer. The decline, despite favourable temperature and light conditions, of production and a shift to decomposition processes in charophyte communities during the second part of summer can be explained by internal factors, such as circannual rhythms. When macroalgal densities exceed a certain critical threshold, growth becomes controlled by internal factors rather than by the biogeochemical environment. Thus, the shift from production to decomposition processes should probably be ascribed to strong self-shading combined with anaerobic conditions within the macroalgal beds (Viaroli *et al.* 1996).

Elongation growth rates exhibited a high correlation with primary production rates. The data on *in situ* primary production rates of charophytes are scarce and often hard to compare due to high spatial and temporal variability (Kufel & Kufel 2002). While the production rate of the apical section in spring and autumn was twice higher than that of the subapical section, during summer the difference remained insignificant. A possible explanation for this could be the slight differences in chlorophyll content in the apical and subapical sections in summer and with similar light conditions (all sections were incubated at the same depth).

According to Libbert and Walter (1985) the photosynthetic activity of *C. tomentosa* is not correlated with temperature, pH or salinity, and the most important environmental factor affecting the photosynthetic activity is solar radiation. Unlike photosynthetic rates, the dark respiration rates of *C. tomentosa* were positively correlated with water temperature. Increased dark respiration at higher water temperatures could thus be a reason for the decrease in the growth rates after midsummer.

The high correlation between the measured elongation growth rate and the calculated primary production rate showed that it is possible to estimate growth on the basis of total carbon uptake. This as well as its reverse relationship enables us to use the data obtained in compiling energy and matter balance models for shallow, vegetation-dominated sea areas.

According to Estonian national monitoring data (database of Estonian Marine Institute) Rame Bay and the adjacent open part of the West-Estonian Archipelago Sea have similar nutrient concentrations. The observed annual dynamics of the nutrient regime in Rame Bay could be explained by biological processes. In such a shallow system the smallest shift from net production to net decomposition will be immediately reflected in water nutrient concentrations.

The information on relationships between nutrient concentrations and the production rates of *C. tomentosa* as well as of other charophytes is highly contradictory. Several authors have described the inhibiting effect of high phosphorus concentrations on the productivity of charophytes (Forsberg 1964, Hough & Putt 1988)
while others maintain that nutrient concentrations below certain thresholds only exert a minor influence on the physiological state (Henricsson 1976, Blindow 1988, Munsterhjelm 2005). Most probably charophyte species are susceptible to indirect effects of nutrient loading, e.g. eutrophication-induced water turbidity and the development of ephemeral macroalgal mats (Blindow et al. 2003). At natural nutrient levels the main factor affecting the productivity of charophytes is solar radiation (PAR) (Libbert & Walter 1985). In the present study the concentration of nutrients remained within the limit values described by other authors as enabling the development of healthy *C. tomentosa* populations (Henricson 2002). As the active growth takes place during a relatively short period at the beginning of summer, the amount of available PAR and the temperature levels during this sensitive time can have a significant effect on the community in the same year.

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