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Comparison of net primary production rates of *Pilayella littoralis* (L.) Kjellm. and other dominating macroalgal species in Kõiguste Bay, northeastern Baltic Sea

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Abstract. *In situ* net primary production measurements by means of the oxygen method were carried out with the ephemeral brown alga *Pilayella littoralis*, which dominates in the benthic vegetation in Kõiguste Bay, NE Baltic Sea. *P. littoralis* was characterized by relatively high net primary production rates (up to 13 $mgO_2\ gDW^{-1}\ h^{-1}$) obtained at 0.5 m depth. In comparison with the perennial algal species *Fucus vesiculosus* and *Furcellaria lumbricalis*, *P. littoralis* had markedly higher (2–5 times on average) net primary production rates. No great differences were found between the maximum net production rates measured for *P. littoralis* and the green alga *Enteromorpha intestinalis.* At the same time markedly higher net primary production rates (peak values reaching 26 $mgO_2\ gDW^{-1}\ h^{-1}$) compared to *P. littoralis* were measured for the opportunistic green algal species *Cladophora glomerata*.

Key words: net primary production rate, *Pilayella littoralis*, *Cladophora glomerata*, *Enteromorpha intestinalis*, *Fucus vesiculosus*, *Furcellaria lumbricalis*, Kõiguste Bay.

INTRODUCTION

Changes in the coastal phytobenthos communities have been documented in different parts of the Baltic Sea during the last decades (e.g. Hällfors et al., 1984; Plinski & Florczyk, 1984; Kautsky et al., 1986; Trei et al., 1987; Vogt &

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Schramm, 1991; Kukk, 1997). With the decline of the perennial (first of all *Fucus vesiculosus*) vegetation a simultaneous increase in filamentous algae has been reported from several parts of the Baltic Sea (Kangas et al., 1982; Haahtela, 1984; Mäkinen et al., 1984; Kukk, 1985; Rönnberg et al., 1985; Kautsky et al., 1986, 1992; Breuer & Schramm, 1988; Baden et al., 1990; Kukk & Martin, 1992; Kiirikki & Lehvo, 1997). The enhanced nutrient contents in the water and decreased water transparency have been considered to favour extensive growth of ephemeral filamentous, predominantly green algal species such as *Cladophora glomerata* and *Enteromorpha* sp. (e.g. Wallentinus, 1978; Kautsky et al., 1986; Baden et al., 1990). However, besides the macroalgal blooms dominated by the above-mentioned green algal species, mass occurrence of the brown alga *Pilayella littoralis* is nowadays an increasingly more frequent phenomenon documented by several authors (e.g. Vogt & Schramm, 1991; Kiirikki & Lehvo, 1997; Lotze, 1998) in the northern as well in the southern Baltic Sea.

In Kõiguste Bay, northeastern Baltic Sea, notable expansion of *P. littoralis* was observed in 1995–98. Up to 1995 the perennial algal species *Fucus vesiculosus* and *Furcellaria lumbricalis* dominated in the benthic vegetation of Kõiguste Bay, but already in 1998 *P. littoralis* was dominant down to 8 m depth. The species occurred as epilithic or epiphytic (mainly on *F. vesiculosus*) at smaller depths and was freefloating at greater depths (Kotta et al., 2000).

In 1997–2001, within the framework of different projects, several *in situ* net primary production measurement series were carried out with different macroalgal species common in the benthic vegetation of Kõiguste Bay. This paper focuses mainly on the comparison of net primary production rates measured for the dominating algal species in the area (*P. littoralis*) and co-occurring species (incl. ephemeral green algae *C. glomerata* and *E. intestinalis* and perennial *F. lumbricalis* and *F. vesiculosus*).

MATERIAL AND METHODS

The *in situ* net primary production (NP) measurements were carried out in Kõiguste Bay, northeastern Baltic Sea (Fig. 1). Kõiguste Bay belongs among the least eutrophied areas of the Estonian coastal sea (Suursaar, 1995).

The algal material – *Pilayella littoralis* (L.) Kjellm. and *Fucus vesiculosus* L. (Phaeophyceae); *Cladophora glomerata* (L.) Kütz. and *Enteromorpha intestinalis* (L.) Nees. (Chlorophyceae); *Furcellaria lumbricalis* (Huds.) J. V. Lamour. (Rhodophyceae) – was collected at depths from 0.5 to 4 m. The net primary production (i.e. net photosynthetic) rates were measured using the oxygen method. Samples of algal material of about 0.05 g (dry weight) were incubated in 600 mL glass bottles (the bottles were large enough to guarantee that depletion of

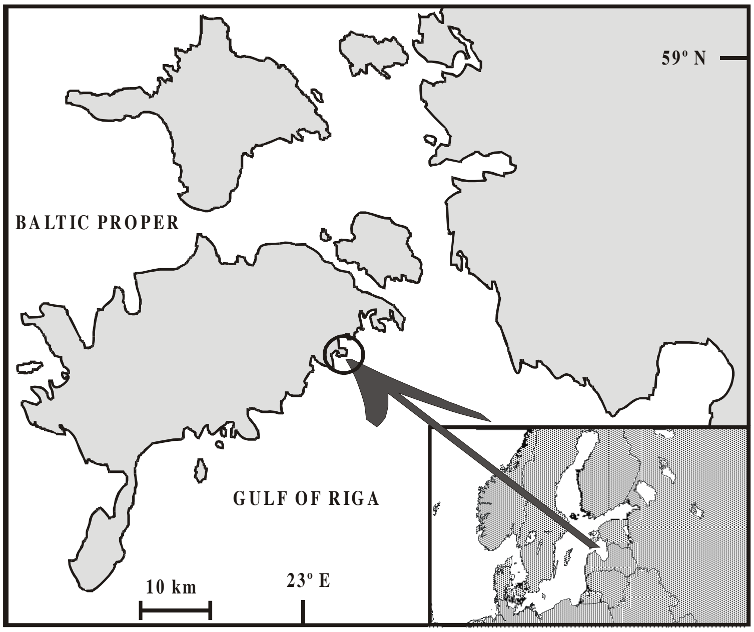


Fig. 1. Study area. The circle shows the location of Kõiguste Bay.

nutrients or carbon did not affect the photosynthetic performance of test algae) filled with seawater. The samples were incubated horizontally on special trays at a depth of 0.5 m. Bottles without algae served as controls.

The changes in the dissolved oxygen concentration were measured by an oxygen meter OXI 92 (Kotta et al., 2000). At the time of the incubation the total insolation above the water surface was measured with a pyranometer. The obtained values were converted to µmol m^{-2} s^{-1} (Lüning, 1981) and transformed to PAR (photosynthetically active radiation) by multiplying with a factor of 0.45 (Bröckel, 1975).

RESULTS

Generally the maximum NP rates of *P. littoralis* varied between 5 and 7 mgO_2 gDW^{-1} h^{-1}, resulting in daily NP rates (i.e. measured over a 24 hour period) up to 66 mgO_2 gDW^{-1} 24 h^{-1}. As a rule NP rates peaked already in April despite the relatively low water temperature i.e. below 12 °C (Figs. 2 and 3a). Somewhat lower NP rates were obtained for *P. littoralis* in May (Fig. 3a). Exceptionally high NP rates for *P. littoralis* – up to 13 mgO_2 gDW^{-1} h^{-1} (112 mgO_2 gDW^{-1} 24 h^{-1}) – were measured in July 2001 (Fig. 4).

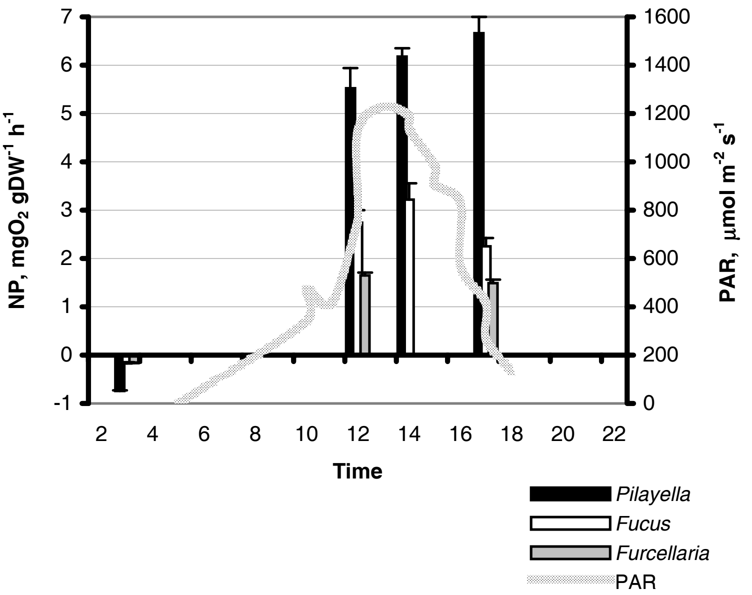
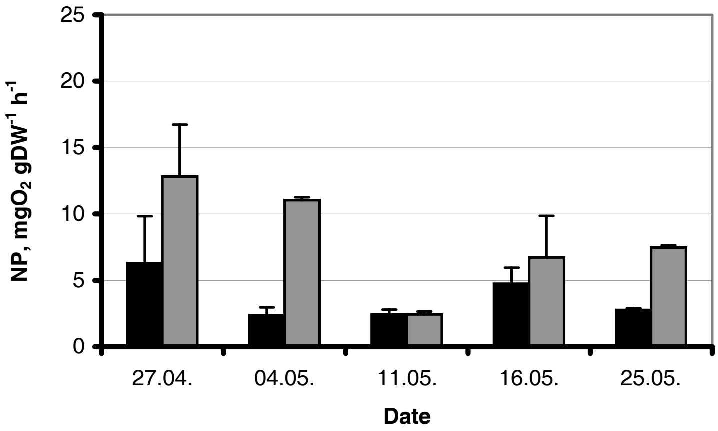


Fig. 2. Diurnal changes of net production (NP) rates (± standard error; *n* = 3) in *P. littoralis*, *F. vesiculosus*, and *F. lumbricalis* plotted against surface PAR readings measured in April at water temperature of 7–12 °C.

In comparison with the perennial algal species *F. vesiculosus* and *F. lumbricalis*, *P. littoralis* was responsible for markedly higher NP. The greatest differences (on average 3–5 fold) in NP rates were found between *P. littoralis* and *F. lumbricalis* during the diurnal incubations performed in April and July. In spring the NP rates of *F. vesiculosus* made up about 50% (Fig. 2) and in summer about 60% of the values measured for *P. littoralis* (Figs. 2 and 5). Much higher NP rates (peak values up to 26 $mgO_2\ gDW^{-1}\ h^{-1}$, i.e. daily NP of 237 $mgO_2\ gDW^{-1}\ 24\ h^{-1}$) compared to *P. littoralis* were measured for the opportunistic green algal species *C. glomerata*. The greatest differences in the NP rates between these species were found in July–August (Figs. 3b and 6).

At the same time no great differences were found between the maximum NP rates measured for *P. littoralis* and the green alga *E. intestinalis* (11 and 13 $mgO_2\ gDW^{-1}\ h^{-1}$, respectively). However, contrary to *P. littoralis*, the NP rates of *E. intestinalis* peaked only in August, resulting in daily NP rates as high as 73.8 $mgO_2\ gDW^{-1}\ 24\ h^{-1}$ (Figs. 4 and 6).

(a)



(b)

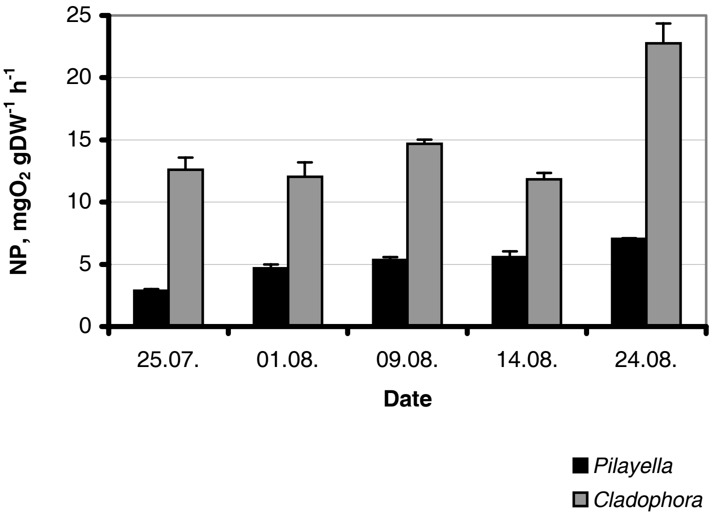


Fig. 3. Changes in maximum net production (NP) rates (± standard error; $n = 3$) measured for *P. littoralis* and *C. glomerata*: (a) in spring (April–May) at water temperature of 11–16 °C and (b) summer (July–August) at water temperature of 17–22 °C.

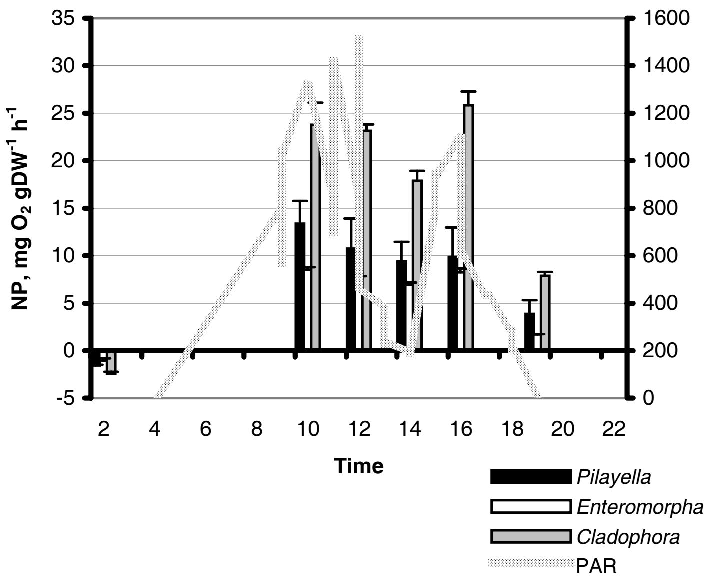


Fig. 4. Diurnal changes of net production (NP) rates (± standard error; $n = 3$) in *P. littoralis*, *E. intestinalis*, and *C. glomerata* plotted against surface PAR readings measured in July 2001 at water temperature of 23–24 °C.

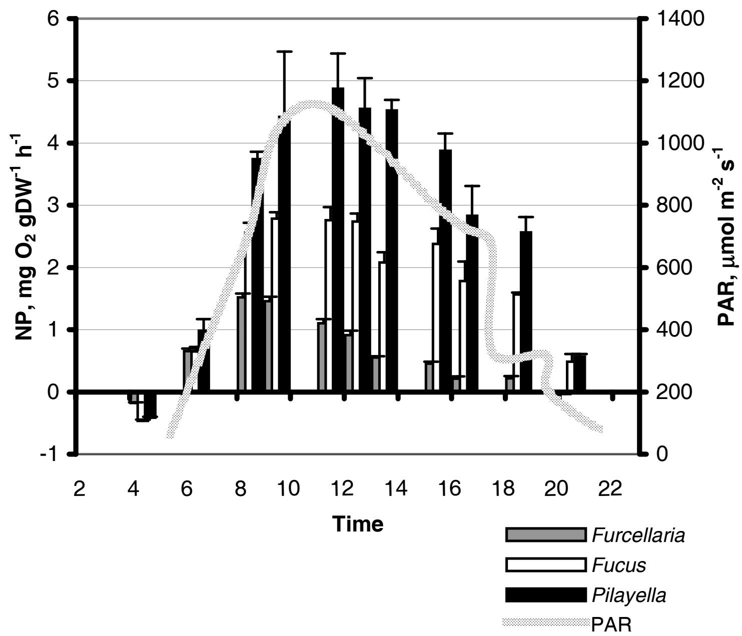


Fig. 5. Diurnal changes of net production (NP) rates (± standard error; $n = 3$) in *P. littoralis*, *F. vesiculosus*, and *F. lumbricalis* plotted against surface PAR readings measured in July at water temperature of 18–22 °C.

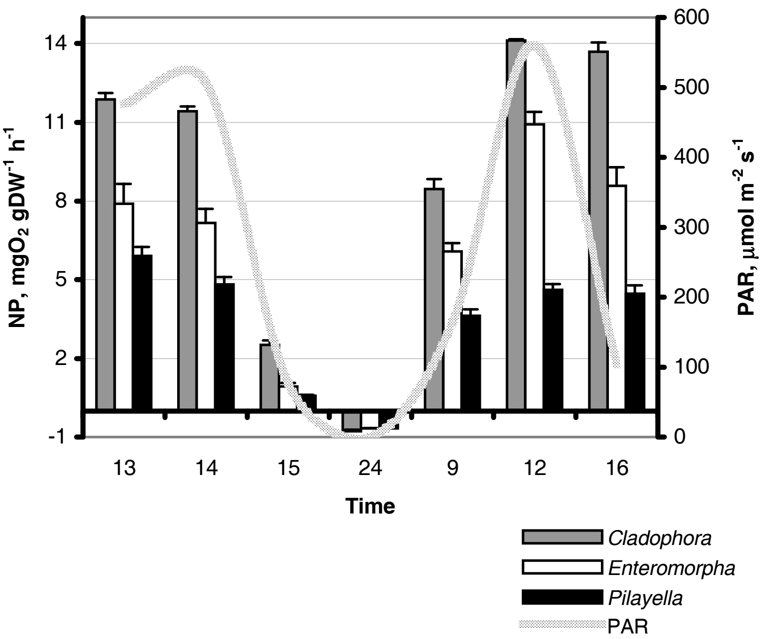


Fig. 6. Diurnal changes of net production (NP) rates (± standard error; *n* = 3) in *P. littoralis*, *E. intestinalis*, and *C. glomerata* plotted against surface PAR readings measured in August at water temperature of 17–22 °C.

DISCUSSION

The *in situ* NP rates measured for *P. littoralis* at 0.5 m depth in Kõiguste Bay may be considered relatively high when compared with perennial algal species such as *F. vesiculosus* and *F. lumbricalis*. However, in comparison with the green alga *C. glomerata*, at least at shallow depths (0.5 m), *P. littoralis* showed notably lower primary production during our experiments.

Differences in the NP between *P. littoralis* and the above-mentioned perennial algal species are most likely determined by the morpho-physiological differences of algal thallus resulting in different growth strategy (Arnold & Murray, 1980; Littler, 1980; Littler & Littler, 1980). Still, attention should be paid also to the fact that naturally *F. vesiculosus* and *F. lumbricalis* inhabit shaded or deeper places being well adapted for growth at low light intensities. High PAR, exceeding at the 0.5 m depth several times the presumed light saturation levels for the above-mentioned species, will probably cause some decline of NP rates due to photoinhibition.

According to the functional-form model both *P. littoralis* and *C. glomerata* are regarded as opportunistic and belonging to the filamentous category (Littler & Littler, 1980). Thus the differences in their photosynthetic capacity cannot be explained by different morphology alone. The colonization of *P. littoralis* has recently been very intensive near the surface in very early spring straight after ice break-up (Kiirikki & Lehvo, 1997). At that time solar irradiation is still at a low level. Unfortunately, we have no data on NP rates from higher depths where similar low irradiation rates prevail, but in the Seili area, SW Finland, remarkably high NP rates have been reported at the depth of 4 m already at the beginning of March at the water temperature below 1 °C (Paalme & Mäkinen, 1997). This indicates that contrary to *C. glomerata P. littoralis* may have been favoured by low solar irradiance and low water temperature during the recent early spring seasons.

At the beginning of our spring experiments in April the water temperature exceeded 10 °C. This together with favourable light conditions may explain the high NP rates of *C. glomerata*. Relatively low NP rates measured for *P. littoralis* in May are most likely due to changes in the physiological state of the alga accompanied with the ageing of algal thallus (incl. degeneration and detachment of filaments).

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Pilayella littoralis'e ja teiste Kõiguste lahes domineerivate makrovetikate primaarproduktsiooni võrdlus

Tiina Paalme ja Henn Kukk

Kõiguste lahe vetikakoosluses domineerivat pruunvetikat *Pilayella littoralis* iseloomustavad suhteliselt kõrged neto-primaarproduktsiooni (NP) väärtused. 0,5 m sügavusel oli *P. littoralis*'e NP tunduvalt kõrgem (keskmiselt 2–5 korda) kui mitmeaastastel vetikaliikidel *Fucus vesiculosus* ja *Furcellaria lumbricalis*. Samal ajal kui liikide *P. littoralis* ja *Enteromorpha intestinalis* NP väärtustes ei täheldatud olulisi erinevusi, oli *Cladophora glomerata* NP märkimisväärselt kõrgem.