

Growth and production rates of loose-lying and attached forms of the red algae *Furcellaria lumbricalis* and *Coccotylus truncatus* in Kassari Bay, the West Estonian Archipelago Sea

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Abstract

Two ecologically and morphologically distinct forms of *Furcellaria lumbricalis* and loose form of *Coccotylus truncatus* were experimentally tested to obtain information on the growth rates and influence of the habitat depth on their eco-physiological activity. Incubations were carried out in the area inhabited by a loose *F. lumbricalis*–*C. truncatus* community in Kassari Bay of the West-Estonian Archipelago Sea, the NE Baltic Sea. During the incubation period (20.04–21.10.2002) loose forms of *F. lumbricalis* and *C. truncatus* showed similar dynamics of both growth rate of biomass and primary production while attached form of *F. lumbricalis* had, as a rule, significantly lower growth rate and primary production values. The highest eco-physiological activity was recorded from the shallowest incubation depth (4 m) for all three algal forms. All three tested algal forms had similar pattern of growth during the incubation period – highest growth rates were detected in spring and early summer while during the rest of the incubation period algal biomass was in a steady state when production balanced degradation processes.

Introduction

In the Baltic Sea at least two ecologically distinguished forms of the red algal species *Furcellaria lumbricalis* (Huds.) Lamour can be found. The attached form of this species is very common on the hard bottoms in the whole Baltic Sea inhabiting the lower part of the phytobenthic zone (Nielsen et al., 1995). Already more than 100 years ago, the loose-lying form was described as common in the inner archipelagos of the Baltic Sea (Svedelius, 1901 and references therein). Large communities of loose-lying *F. lumbricalis* on the contrary is very unique – up to the present only three localities have been described in the Baltic Sea as having large communities of this form, one of these (Puck Bay) already lost the population

due to eutrophication and pollution problems (Kruk-Dowgiallo & Cisewski, 1994; Martin et al., 1996). Austin (1959) described similar agglomerations of loose *Furcellaria* in the central Kattegat area. The sea area of West Estonian Archipelago hosts the largest known community of this kind where a mixed community of loose-lying *F. lumbricalis* and *Coccotylus truncatus* (Pall.) M. J. Wynne & J. N. Heine covers up to 120 km² of sea bottom and forms more than 140 000 tons of biomass in Kassari Bay. The community was described for the first time by Kireeva (1961, 1964). The mean biomass of this community varied between 500 and 1000 g of wet weight m⁻² and occasionally reached maximum of 2.1 kg wet weight m⁻² (Trei, 1975, 1976; Martin et al., 1996). The community was found on sandy substrates at

the depth between 5 and 9 m, where it formed a 0.15–0.3 m thick carpet on the seafloor. The proportion of the two main dominant species differs slightly depending on locality but usually 60–70% of the biomass was made up by *F. lumbricalis*, while *C. truncatus* accounted for 30–35%, on average. The share of other species was usually low, less than 5% (Trei, 1975, 1976; Martin et al., 1996).

This loose-lying red algal community has been used as raw material for 'agar' (=furcellaran) production already from 1966 and annual catches has been estimated to be near 1000 t of wet weight. State of the community has been monitored regularly and a drastic decline of the loose *F. lumbricalis*–*C. truncatus* community was recorded in the Kassari Bay of the Väinameri area during 1996–1997. The decline of this loose-lying red algal community was explained to be due to the extensive overgrowth by filamentous brown algae, fixing the algae carpet and causing oxygen deficiency in the nearbottom layer (Martin & Kukk, 1997a, b, 1998, 1999).

The aim of this study was (1) to experimentally compare the growth rates of the two different forms, i.e. loose-lying and attached forms of *F. lumbricalis* (Huds.) Lamour, and *C. truncatus* (2) to estimate the dependence of growth rate and

primary production of the algae on depth (3) to follow seasonal changes in production rates.

Material and methods

Study area

Väinameri (inner sea of the west-Estonian archipelago) is formed by a system of straits connecting the waters of the Gulf of Riga to the Baltic proper and the entrance to the Gulf of Finland (Fig. 1). The total surface area of the system is 2243 km² and the total volume 10.6 km³ (Suursaar et al., 1998). This sea area is characterised by its shallow waters. The mean depth of the whole system is less than 10 m with the deepest location at 22 m in the middle of the Suur Strait. The general water exchange processes are highly dependent on the shallowness of the sea (minimum sill depth 5 m on the Suur Strait – Hari Kurk direction). Due to the numerous shallow bays and the grid of small islets the area could be divided into two more or less independent waterbodies. Kassari Bay, in the western part of the area, is connected to the Baltic proper through the narrow Soela Strait and separated from the eastern part by a grid of islets. Hydrologically, this area behaves differently from

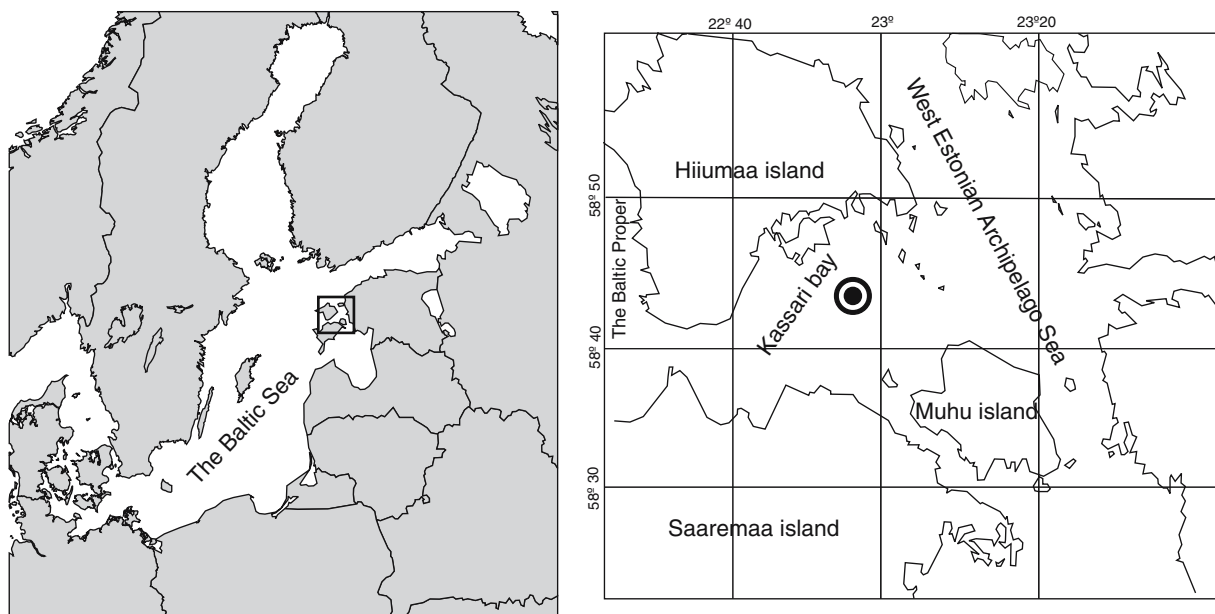


Figure 1. Study area. Incubation site marked.

the other parts of the Väinameri as it is more influenced by the saline waters of the Baltic proper (Suursaar et al., 1998). The system of Hari Strait – Suur Strait is strongly influenced by the water-masses originating from the Gulf of Riga (Suursaar et al., 1998). The impact of the riverine inflow on the system is very small, because the amount of fresh water entering the system reaches only $1 \text{ km}^3 \text{ yr}^{-1}$ (Astok et al., 1999). Suursaar et al. (1998) point out to the existence of a strong hydrological front of Väinameri which has a number of subfronts moving rapidly over the whole area depending on the wind-induced water movement between the Gulf of Riga and the entrance to the Gulf of Finland. Thus, the basic hydrochemical characteristics can fluctuate within a wide range depending on the origin of the water filling the basin. The seafloor is mainly composed of soft sediments including fine mud and sand fractions. Harder substrates as gravel or boulders can be found only in the most shallow and wave exposed areas. Due to the shallowness and the bottom substrate being dominated by fine sediment fractions, the water transparency is often very poor. After storm events the Secchi depth may decrease to 0.5 m, while in the case of prolonged calm weather conditions the photic zone reaches the bottom in about 90% of this area.

Field experiments

Field experiments for estimating the growth rate of loose-lying and attached forms of *F. lumbricalis* (Huds.) Lamour and *C. truncatus* (Pall.) M.J. Wynne & J.M. Heine were carried out between 20.04.02. and 21.10.02. in Kassari Bay (Fig. 1). *In situ* incubations of algal material were performed in special nylon mesh bags (with plastic frame inside; \varnothing 5.5 cm, height 20 cm) of 1 mm mesh size. The light decrease inside the nylon mesh bags compared to outside was in the same order of magnitude as the decrease in light in algal mat due to the self shading effect. Mesh bags with freshly collected algae (about 2–5 g wet weight) with no macroepiphytes were incubated at three different depths – 4, 6 and 8 m (Fig. 2). Once a month 3×5 replicates of each species were collected for determination of growth rate. The changes in algal biomasses are presented as percent algae remaining from the initial value (mean \pm SE). Relative

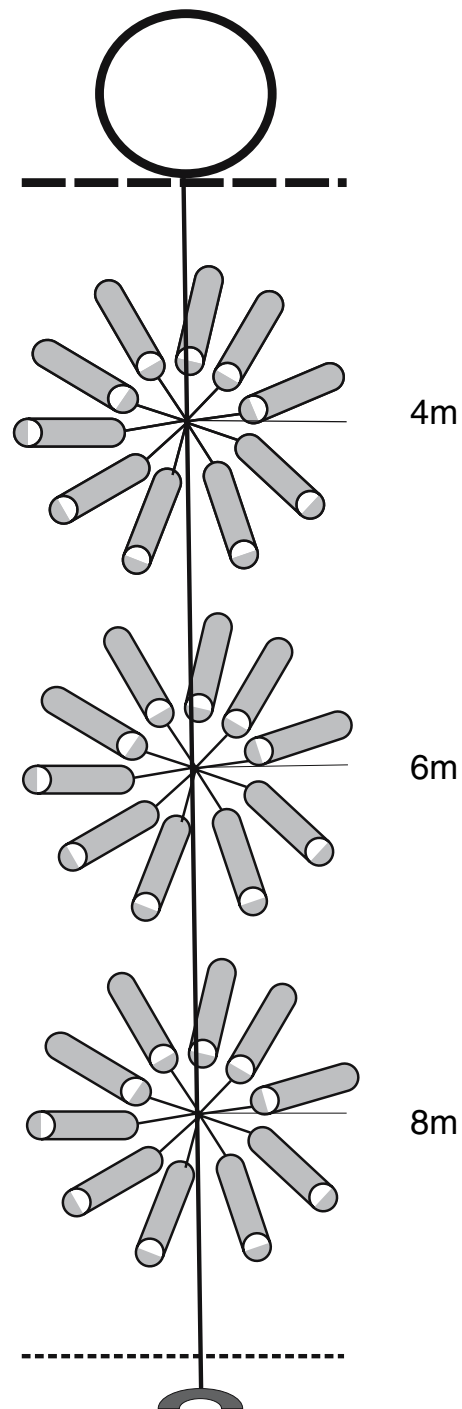


Figure 2. Illustration of experimental setup.

daily growth rates (DGR) were calculated for six experimental periods: 20.04.–22.05. (I); 22.05.–19.06. (II); 19.06.–20.07. (III); 20.07.–22.08. (IV);

22.08.–16.09. (V) and 16.09.–21.10. (VI). The equation: $DRG (\%) = [(\ln W_1 - \ln W_0) / n - 1] 100$, where n is the number of days of the incubation period, W_1 and W_0 are the final and the initial weight of the algal material, respectively, was used.

For estimating the physiological status of algal material on different phases of the growth, net photosynthetic rates were measured using oxygen method. For this procedure about 0.1 g (dry weight) of algal material were incubated in 600 ml glass bottles, filled with the sea water and incubated horizontally on special transparent trays hanging at 4, 6 and 8 m depth. Bottles without algae served as controls. During a 24-h period every third hour the water in the incubation bottles was changed (to avoid the depletion of carbon or nutrients and over saturation by oxygen). The changes in dissolved oxygen concentrations were measured by an oxygen meter OXI 92. Daily net primary production (NP_{24}) rates are calculated as the sum of several incubation periods (Kotta et al., 2000).

At the time of the incubations the total insolation above the water surface and water temperature at incubation depths were measured. The obtained values of total insolation were converted to $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Lüning, 1981) and transformed to PAR (photosynthetically active radiation) by multiplying with a factor of 0.45 (Bröckel, 1975). Water transparency was estimated by Secchi disc.

Results

Environmental parameters

During the observation period the water transparency was low, as a rule not exceeding 2 m (Table 1).

The water temperature at incubation depths varied between 0.5 and 22.8 °C, measured in October and July–August, respectively (Table 1).

Growth rates

The highest growth rates during the investigation period for loose-lying and attached forms of *F. lumbricalis* as well for *C. truncatus* were obtained at the incubation depth of 4 m, resulting in a final increase of initial biomasses (on dry weight

Table 1. Changes in water transparency (Secchi depth), water temperature at incubation depths and daily maximum of PAR at the water surface

Date	Transparency (m)	Temperature (°C)		PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
		Min	Max	
20.04.	2.0	5.7	6.4	1323
22.05.	1.9	13.3	14.5	1550
19.06.	2.3	11.3	14.6	1455
20.07.	1.8	21.9	22.8	454
22.08.	1.8	21.4	22.8	1493
16.09.	3.5	14.2	16.2	1191
22.10.	1.0	0.5	1.8	284

bases) by 268, 155 and 238%, respectively (Fig. 3). At the depths of 6 and 8 m the biomass increment was remarkably lower, whereas at all three incubation depths the lowest values were measured for attached form of *Furcellaria* (Fig. 3).

A significant seasonal variation in the relative DRG at all incubation depths was found (Fig. 4). At the 4 m depth no great differences in DRG values (varied between 1.1 and 1.6%) were obtained for loose-lying *Furcellaria* during the first 4 months of incubation, while at the depths of 6 and 8 m the continuous increase of DRG values (up to 2.0%) was observed from the beginning of investigation period until the end of the III period (end July) and was followed by a rapid decrease in growth rates in August–September (IV–V period). The most pronounced increase in DRG of attached *Furcellaria* (up to 2.7%) was recorded in June–July (III period) at all incubation depths. In the same period the peak DRG values (1.7–1.9%) of *Coccotylus* were obtained.

During the IV period, remarkable increase of biomass was obtained only at 4 m depth for loose-lying *Furcellaria* and *Coccotylus*, while the biomass of attached *Furcellaria* decreased. The lowest (negative) DRG values for all species were obtained in V period (Fig. 5) resulting in remarkable decline of the biomass (Fig. 4).

Primary production

Daily net primary production (NP_{24}) rates (i.e. measured over a 24 h period) of loose-lying *Furcellaria* and *Coccotylus* reached maximum values (up to 13.7 and 12.4 $\text{mg O}_2 \text{g}_{\text{dw}}^{-1} 24 \text{h}^{-1}$ at 4 m

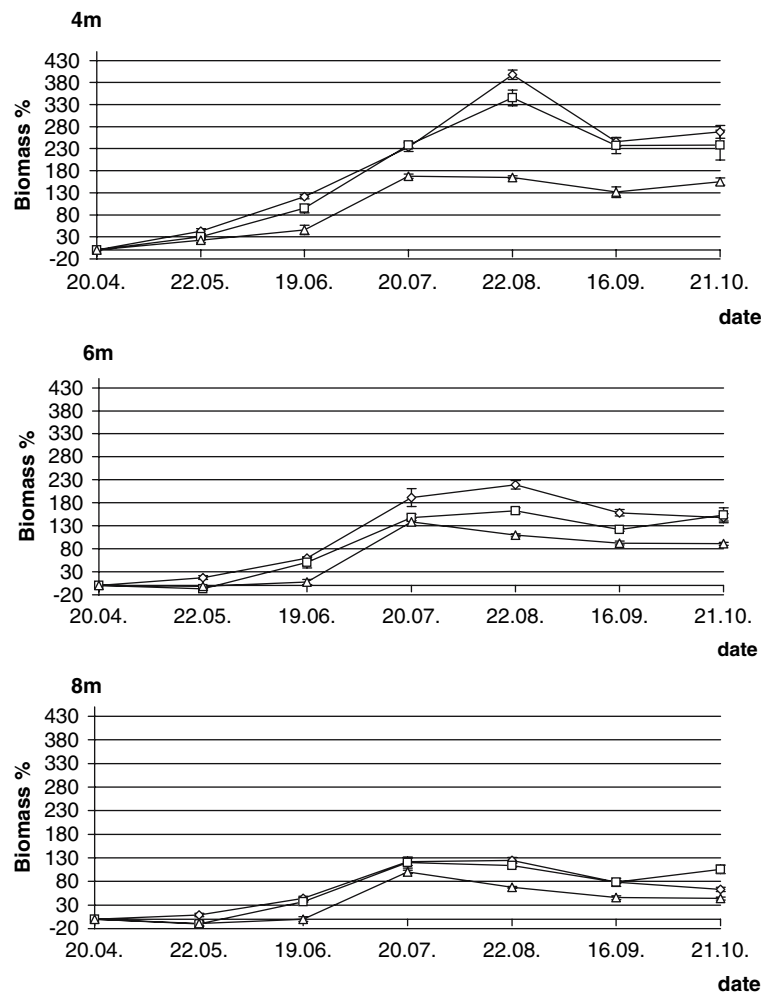


Figure 3. Gain of biomass (expressed as per cent of initial algal dry weight \pm standard error, $n = 5$) obtained for loose-lying *Furcellaria lumbricalis* (-◇-), attached *F. lumbricalis* (-Δ-) and *Coccotylus truncatus* (-□-) at the depths of 4, 6 and 8 m.

depth) in May–June (Fig. 5). By using a PQ value of 1.2 these production rates correspond to 4.3 and 3.9 $\text{mg C g}_{\text{dw}}^{-1} 24 \text{ h}^{-1}$, respectively. NP_{24} rates of attached *Furcellaria* peaked in June (10.3, 5.9 and 4.6 $\text{mg O}_2 \text{ g}_{\text{dw}}^{-1} 24 \text{ h}^{-1}$ measured at depths of 4, 6 and 8 m accordingly). These rates would correspond to 3.2, 1.8 and 1.4 $\text{mg C g}_{\text{dw}}^{-1} 24 \text{ h}^{-1}$, respectively. During the entire investigation period the highest NP_{24} rates were obtained at 4-m depth.

Discussion

In our study both incubation period and incubation depth affected significantly the growth rates of

loose-lying and attached forms of *Furcellaria* as well *C. truncatus* (2-way-ANOVA; $p < 0.001$). At the depth of 4 m the gain of biomass for all studied species was remarkable higher compared to 6 and 8 m indicating the more favourable growing conditions at shallower depths. In natural conditions, on the contrary, most of the loose-lying *Furcellaria*–*Coccotylus* community is found inhabiting a depth of 6–9 m (Martin et al., 1996). The contradiction can be explained by several other limiting environmental factors as wave activity, biological interactions, etc. keeping most of the loose algal community deeper. Most of the added biomass compared to the initial condition was gained during the first half of the observation period and the

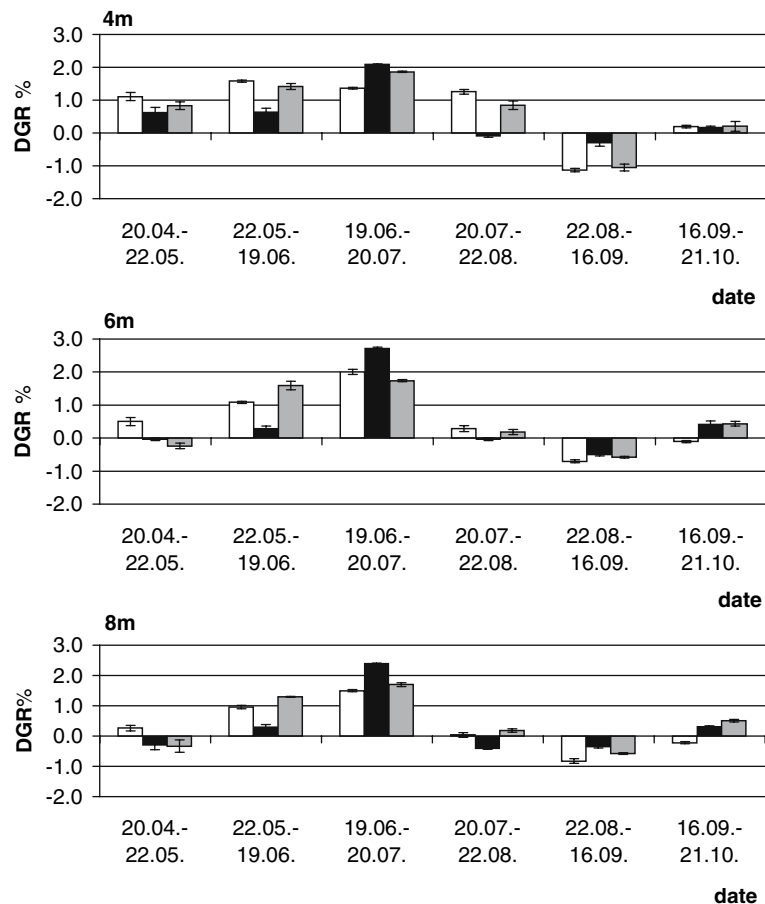


Figure 4. Relative daily growth rates (DRG; expressed as percentage of daily dry weight increase of algal material \pm standard error, $n = 5$) of loose-lying *Furcellaria lumbricalis* (white bars), attached *F. lumbricalis* (black bars) and *Coccotylus truncatus* (grey bars) measured at the depths of 4, 6 and 8 m.

pattern was similar to all three studied forms. So it could be assumed that most of net annual production of the natural algal communities is achieved during the spring and beginning of summer. According to literature data it is also true for many other macroalgal species (Kiirikki, 1996).

Our maximum daily productivity rate for loose-lying *Furcellaria* is slightly lower than was measured by Wallentinus (1978: Fig. 8), who in May measured around $4.6\text{--}5.4 \text{ mg C g}_{\text{dw}}^{-1} 24 \text{ h}^{-1}$ by using the ^{14}C -method which, however, might give data somewhat higher than true net production. If short-term measurements are compared (i.e. daily values divided by 24, giving $\text{mg C g}_{\text{dw}}^{-1} \text{ h}^{-1}$) our values are about half of or lower than her rates (Wallentinus, 1978: Table II). Furthermore, the Pmax-value obtained by Johansson & Snoeijs,

(2002), when using a Light Dispenser System, were more than four times higher than our values, if recalculated to the same units.

Biomass dynamics of loose-lying *Furcellaria* and *Coccotylus* during the entire experimental period followed quite a similar pattern at all incubation depths, reaching the highest biomass in August. Loose-lying *F. lumbricalis* and *C. truncatus* form together a unique mixed community in Kassari Bay and thus are most probably adapted to similar environmental conditions.

Compared to loose-lying *Furcellaria* and *Coccotylus*, the final biomass of attached *Furcellaria* was significantly lower at all incubation depths. Attached *Furcellaria* was characterised also by a very rapid growth during the III experimental period, while afterwards no remarkable biomass

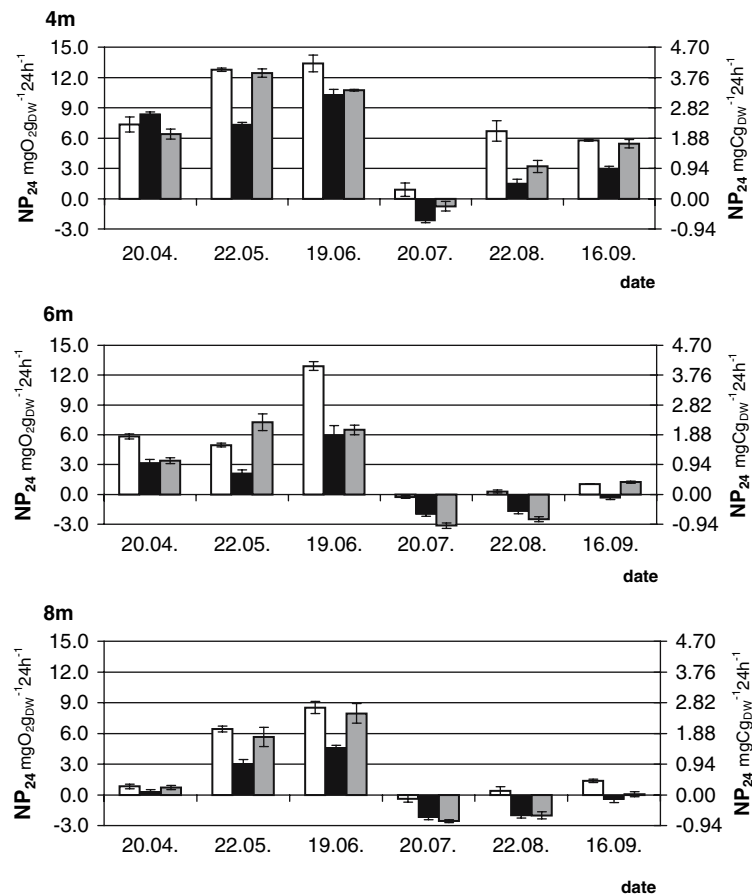


Figure 5. Daily net production rates (NP₂₄; ± standard error, n = 3) of loose-lying *Furcellaria lumbricalis* (white bars), attached *F. lumbricalis* (black bars) and *Coccotylus truncatus* (gray bars) measured at the depths of 4, 6 and 8 m.

increment took place. In Kassari Bay, where soft bottoms of chiefly clay and sandy clay prevail (Trei, 1978) the water transparency can change very rapidly depending on weather conditions. Due to decreased light penetration through the water column the presumed light saturation point for photosynthesis of attached Baltic *F. lumbricalis* – 116 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (Johansson & Snoeijs, 2002) could be reached for a very short period and most likely only at shallower depths (4 m depth in case of our study). However, Wallentinus (1978: Fig. 2a) using Baltic *Furcellaria* found that the light saturation points varied between seasons and in autumn–winter–spring could be as low as around 50–60 $116 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, whereas in June a maximum of ca. 160 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ could be obtained. The upward shift of attached *F. lumbricalis* population due first of

all to worsened light conditions have been pointed out by several authors (e.g. Mäkinen et al., 1988).

Compared to attached *Furcellaria*, the light saturation point obtained for Baltic *C. truncatus*, is remarkably lower – 69 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (Johansson & Snoeijs, 2002), thus giving latter an advantage to inhabit deeper areas. Wallentinus (1978: Fig. 2b) found for Baltic *Coccotylus* similarly low light saturation points in winter–spring of around 50–60 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (no June measurements were performed). In our case, the loose form of *Furcellaria* must have also developed similar characteristics as the behaviour in the nature and our experiment showed very close similarity for loose *Furcellaria* and *Coccotylus*.

In the second half of the investigation period the slight decline of biomass was observed for all species most probably due to the onset of

decomposition processes in the algal material. The latter was likely to be favoured by relatively high water temperature, since as a rule decomposition processes are dependent on temperature (Carpenter & Adams, 1979; Birch et al., 1983). Besides high water temperature, losses of algal biomass could also be attributed to low photosynthetic activity of the algae caused first of all by low water transparency due to increased pelagic productivity during this warm period. It was remarkable that the high temperature values had similar effect on all three studied algal forms.

One of the main conclusions from the experiment is that the attached and loose forms of *Furcellaria* have a significant difference in eco-physiological characteristics. The influence of experimental design on the results with removal of attached plants from substrate cannot be the cause of the differences as attached *Furcellaria* is known to have a high capacity of reattaching by secondary rhizoids (Johansson & Eriksson, 2002).

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