



## Does the growth rate of drifting *Furcellaria lumbricalis* and *Coccotylus truncatus* depend on their proportion and density?

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**Abstract.** The West Estonian Archipelago Sea hosts a loose-lying red macroalgal community dominated by *Furcellaria lumbricalis* and *Coccotylus truncatus*. The community is truly unique in European seas. In factorial field experiments we evaluated separate and interactive effects of algal density and the proportions of *F. lumbricalis* and *C. truncatus* on their growth rates in a set of monospecific and mixed communities. Our experiment demonstrated that the growth of red algae was density dependent and that increased algal densities resulted in a fall of daily growth rates. An elevated growth of the red algae was observed at their lower proportions in the community. A potential mechanism behind the observed patterns is the light availability for photosynthesis, i.e. light utilization is more efficient in mixed communities.

**Key words:** marine biology, loose-lying macroalgae, Rhodophyta, growth rate, density dependence, Baltic Sea.

### 1. INTRODUCTION

Earlier observations and experimental work suggest that complex interactions between varieties of processes regulate marine benthic communities (Pianka, 1971; Ricklefs and Schluter, 1993; Rosenzweig, 1995). Menge and Sutherland (1987) proposed that the development of benthic assemblages is primarily due to three major regulating forces: environmental disturbance, competition, and predation. Competition arises when species compete for a short supply of a resource or space. Marine benthic macroalgae are known to compete mainly for light, space, and/or nutrients (e.g. Lobban and Harrison, 2000). Elevated competition among algae results in slower growth rates and/or reduced density as a consequence of the self-thinning phenomenon (Reed, 1990; Rivera and Scrosati, 2008).

Despite a large body of literature, biotic interactions between marine macroalgae are little understood. Only a few studies on exploitative competition between sea-

weeds have been performed in laboratory (e.g. Russell and Fielding, 1974; Enright, 1979) and even fewer in field conditions (Dudgeon et al., 1999; Kim, 2002; Piazzini and Ceccherelli, 2002). Interspecific interactions among macroalgae have been addressed mainly in hard-bottom habitats whereas studies in soft-bottom communities are very rare (Albrecht, 1998). Marine macrophyte communities are among the most productive habitats worldwide and they provide important functions for ecosystems and services for human beings (Micheli and Peterson, 1999; Duarte, 2002; Ince et al., 2007). Thus, there is a need for in situ experimental studies that quantify the importance of biotic interactions among macroalgae in order to improve our understanding on the patterns of productivity of marine macrophyte communities.

The West Estonian Archipelago Sea, the Baltic Sea, hosts a loose-lying red macroalgal community dominated by *Furcellaria lumbricalis* (Hudson) J. V. Lamouroux and *Coccotylus truncatus* (Pallas) M. J. Wynne & J. N. Heine (Paalme et al., 2011). While both are relatively similar in morphology and characterized by

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irregularly branched thalli without radial symmetry and no organs for attaching and reproduction (Fig. 1), the loose-lying *C. truncatus* have narrow more delicately entangled thalli compared to those of the loose-lying *F. lumbricalis* (Trei, 1978). Thus, the red algal species vary manifold in their compactness, i.e. the biomass to volume ratio is higher for *C. truncatus* than for *F. lumbricalis*.

The community is truly unique in European seas. Unlike the common attached *F. lumbricalis*, the loose-lying form of the species is sterile and reproduces only vegetatively, mainly by fragmentation (Austin, 1960; Norton and Mathieson, 1983; Bird et al., 1991). Population density and the share of the red algal species are not distributed uniformly but vary both spatially and temporally. On average, *F. lumbricalis* accounts for 60–70% of the biomass and *C. truncatus* for 30–35% (Martin et al., 2006a).

Earlier studies have suggested that abiotic environmental factors such as temperature and light conditions drive the dynamics of *F. lumbricalis* and *C. truncatus* (Martin et al., 2006a, 2006b). These results may be incomplete as the experimental design did not allow incubating the two species together and did not include different density levels. Thus, the density-dependent growth due to self-shading was most likely ignored. Although both algal species inhabit a similar niche and have a high potential for interspecific competition for resources, these algae have never been found growing in

monospecific stands in Kassari Bay (Martin et al., 2006a). This points to beneficial interactions between the red algal species.

In low-light environments the efficiency of light use inside communities depends not only on the density but also on the spatial (three-dimensional) structure of the community (Middelboe and Binzer, 2004; Sand-Jensen et al., 2007). It is expected that the light utilization is more efficient in multi-species communities than in single-species communities, resulting in higher photosynthetic rates of multi-species communities both at low and high canopy densities (Middelboe and Binzer, 2004). Thus, ‘supplementing’ one another spatially (making the local environment more favourable for other species), species co-occurrence can counteract to a certain extent the effect of the density-dependent reduction in algal growth rates.

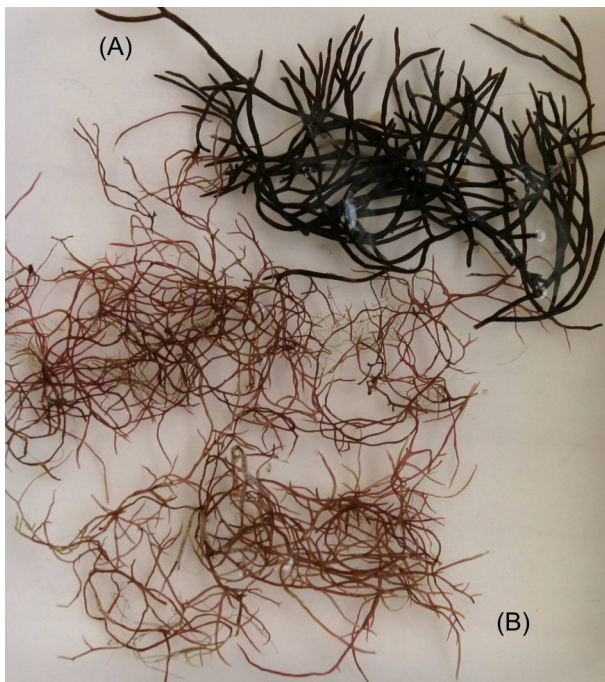
Based on the above, the aim of the study was to experimentally assess the density-dependent growth of the loose-lying red algae *F. lumbricalis* and *C. truncatus* in a set of monospecific and mixed communities. Our hypotheses were as follows: (1) algal growth is inversely related to their density as light limitation increases with algal density; (2) algal growth is higher in mixed communities than in monospecific stands due to improved light conditions within mixed communities.

## 2. MATERIAL AND METHODS

The West Estonian Archipelago Sea is a hydrodynamically very active water basin. Sand and sandy clay substrates prevail in the study area. Due to the shallowness and clayey sediments already moderate winds result in strong resuspension of bottom sediments and poor underwater light conditions there. Salinity in this shallow area varies between 6 and 7 (Kotta and Orav, 2001; Kotta et al., 2008a).

The natural loose-lying community of *Furcellaria lumbricalis* and *Coccotylus truncatus* inhabits sandy substrata at 5 to 9 m depth and forms an up to 0.3 m thick carpet on the seafloor (Martin et al., 2006a). The community covers up to 200 km<sup>2</sup> with more than 200 000 tonnes of wet biomass (Paalme et al., 2011). The community is maintained by the prevailing circular currents and the group of islets that surround the area. *Furcellaria lumbricalis* is the only economically important algal species in the Baltic Sea. It has been exploited for extraction of polysaccharides in the area since the 1960s (Tuvikene, 2009).

The red algal growth was estimated in a factorial field experiment in the West Estonian Archipelago Sea (22°56'43"E, 58°42'0"N). The freshly collected *F. lumbricalis* and *C. truncatus* were instantly cleaned from macroepibionts, weighed, placed in nylon mesh bags (with plastic frame inside, diameter 5.5 cm, height



**Fig. 1.** Still photographs of the loose-lying forms of *Furcellaria lumbricalis* (A) and *Coccotylus truncatus* (B) collected from the West Estonian Archipelago Sea.

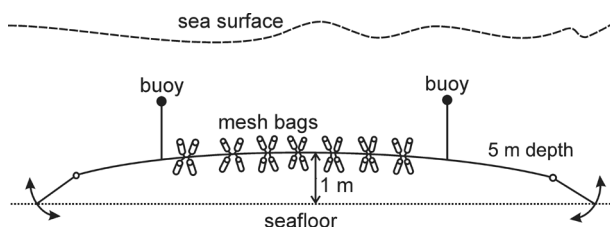
20 cm, 1 mm mesh size), and incubated at 5 m depth (at 1 m above the red algal community) for two months from 18 May to 19 July 2007 (Fig. 2). The algae were deployed at low ( $0.010 \text{ g cm}^{-3}$ ), medium ( $0.025 \text{ g cm}^{-3}$ ), and high densities ( $0.050 \text{ g cm}^{-3}$ ). The volume ratio of *F. lumbricalis* to *C. truncatus* was set at 0:100, 25:75, 50:50, 75:25, and 100:0 in the experiment. Algal densities and proportions represented the realistic values in field conditions (Kotta et al., 2008b; Kersen et al., 2009). Each combination of treatment levels had five replicates (total  $n = 75$ ). Our design allowed water exchange between algae and the ambient environment. Prior to the growth experiment a pilot study was performed to evaluate light conditions at different algal densities and shares of *F. lumbricalis* and *C. truncatus*. Photosynthetically active radiation (PAR) was measured with a LiCor sensor beneath the algal layer of 5 cm at the incubation depth of the growth experiments.

Prior to the growth experiment the wet weight of algae was determined to the nearest of 0.01 g. Before weighing the algae were gently dried on blotting paper until the paper did not become wet any more. Additional five replicates of each macroalgal treatment served as control to obtain the ratio of wet to dry weight (the algae were dried at  $60^\circ\text{C}$  during 48 h; the ratio differed among replicates  $<0.3\%$ ). At the end of the incubation period the dry weight of the remaining algal material was measured. The relative daily growth rates of both algae (DGR) were calculated using the following equation:

$$\text{DGR}(\%) = [(\ln W_1 - \ln W_0)/(n-1)] \times 100,$$

where  $n$  is the duration of the incubation period in days,  $W_1$  and  $W_0$  are the final and the initial dry weight of the algal material in g.

Two-way analysis of variance (ANOVA) was performed to separate the effects of species-specific algal share (percentages of *F. lumbricalis* and *C. truncatus* in the community were 25, 50, 75, and 100) and density levels (low, medium, and high) on DGR. Bartlett's test



**Fig. 2.** Experimental setup (not to scale). Red algae *Furcellaria lumbricalis* and *Coccolytus truncatus* were incubated in nylon mesh bags fastened to a rope, anchored to the bottom, and kept using underwater buoys at 5 m depth ca 1 m above the red algal bed in the West Estonian Archipelago Sea from 18 May to 19 July 2007.

was carried out prior to the analyses and the results confirmed the assumption of homoscedasticity (i.e. homogeneity of variance). Post-hoc Bonferroni test was used to analyse which treatment levels were statistically different from one another (Sokal and Rohlf, 1981).

### 3. RESULTS

Algal density and proportions separately and interactively affected the growth of red algae (Table 1). The growth of both species was significantly reduced at the highest density level (post-hoc Bonferroni test: high density vs. medium and low density levels  $p < 0.001$ ). Both species showed the highest growth rates in mixed communities at their proportion of 25% (post-hoc Bonferroni test: species proportion of 25% vs. 50%, 75%, and 100%  $p < 0.001$ ).

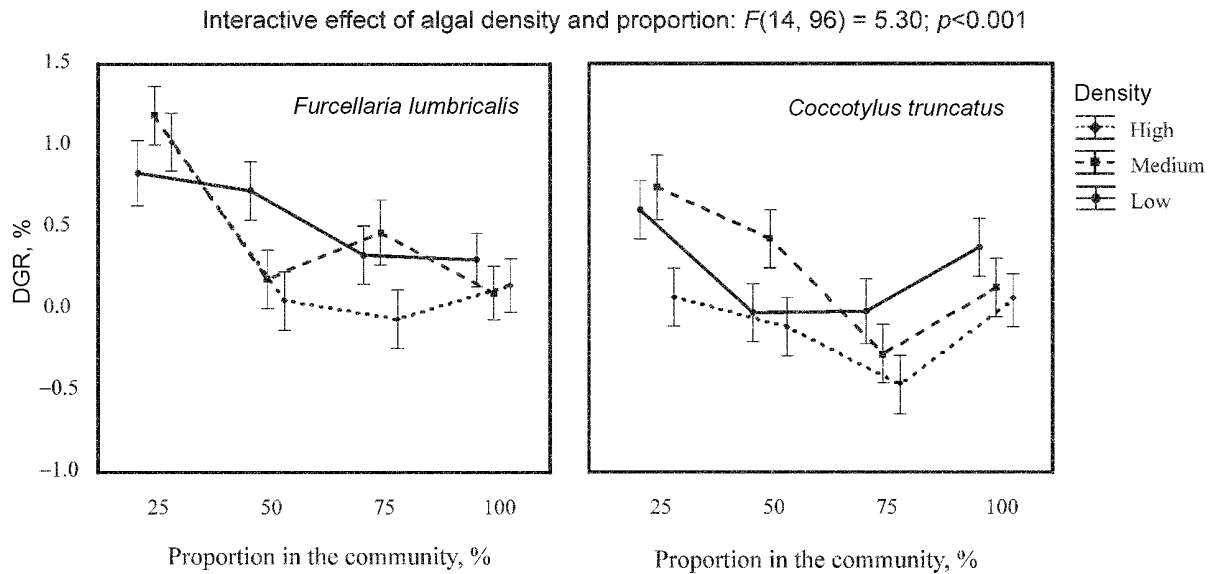
The effect of the species' proportion on the growth rate depended on algal density (Fig. 3). In the monospecific community of *F. lumbricalis*, the algal growth rate was not affected by density. Interactive effects of density and algal proportion on DGR of *F. lumbricalis* were most pronounced at its proportion of 50% (post-hoc Bonferroni test: low density vs. medium and high density levels  $p < 0.001$ ) and 75% (post-hoc Bonferroni test: low and medium density vs. high density levels  $p < 0.001$ ).

The growth rates of *C. truncatus* were significantly reduced in monospecific as well in mixed communities at the highest density level compared to low and/or medium density levels (post-hoc Bonferroni tests:  $p < 0.001$  at the shares of 100% and 75% for low vs. high, at the proportion of 50% for medium vs. high and low, at the proportion of 25% for low and medium vs. high density levels).

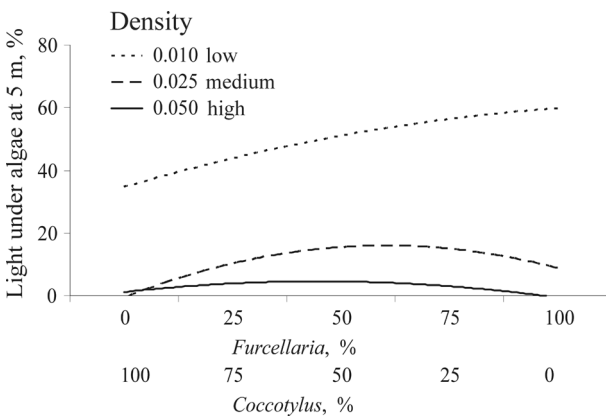
Light conditions beneath the red algae differed among algal species, their density levels, and proportions. At the same densities *C. truncatus* filtered out more light than *F. lumbricalis*. For both algal species, there was an inverse relationship between algal density and light intensities beneath the red algae. Mixed communities had improved light conditions compared to monospecific communities, but this held true only at medium and high densities. At low densities the intensity of light beneath the red algae almost linearly increased with the percentage of *F. lumbricalis* in the community (Fig. 4).

**Table 1.** Two-way factorial ANOVA analysis on the separate and combined effects of species-specific algal proportions and density on the growth of *Furcellaria lumbricalis* and *Coccolytus truncatus*. Significant effects are indicated in bold

Effect	DF	MS	F	p
Proportion	7	1.81	45.75	<b>&lt;0.001</b>
Density	2	1.13	28.49	<b>&lt;0.001</b>
Proportion $\times$ Density	14	0.21	5.30	<b>&lt;0.001</b>



**Fig. 3.** The relative daily growth rates of *Furcellaria lumbricalis* and *Coccotylus truncatus* at their different percentages and density levels. The vertical bars denote 0.95 confidence intervals.



**Fig. 4.** Reduction of PAR (%) by macroalgal mats at different density levels and percentages of *Furcellaria lumbricalis* and *Coccotylus truncatus*.

#### 4. DISCUSSION

The experiment showed that the growth of *Furcellaria lumbricalis* and *Coccotylus truncatus* was density dependent and that the algal growth decreased with increasing densities. On the other hand, the addition of either species counteracted such density-dependent reduction in growth and, thus, the co-existence reduced intra-specific competition. The presence of *C. truncatus* had a positive effect on the growth of *F. lumbricalis* at all densities except for a reduced growth at the medium density and 50% algal share, whereas the presence of *F. lumbricalis* had a positive effect on the growth of *C. truncatus* at medium and low algal densities.

This suggests that density-dependent resource competition determines the growth of *F. lumbricalis* and *C. truncatus* in the study area. The relative strength of the intra- and interspecific competition depended on densities and species percentage. This suggests different efficiencies of light use among communities related to the variability in canopy density and structure (Binzer and Sand-Jensen, 2002; Sand-Jensen et al., 2007).

Competition for space, light, and nutrients is the classical mechanism through which populations of macroalgae are regulated (Lobban and Harrison, 2000). In general, the intensity of competition increases with density (Ang and De Wreede, 1992; Choi and Norton, 2005). High intra- and/or interspecific densities can lead to reduction in the survival, growth, and reproduction of competitors because of competition for limiting resources (Creed et al., 1996, 1997; Choi and Norton, 2005).

There exists experimental evidence that the growth of red algae is light limited in the West Estonian Archipelago Sea (Martin et al., 2006a). Due to the shallowness and domination of fine sediment fractions in the bottom substrate the water transparency in the study area is often very poor (Kotta et al., 2008b). After storm events the Secchi depth may decrease to 0.5 m and the light conditions are often suboptimal for the red algal growth. Competition for nutrients is not likely as the West Estonian Archipelago Sea is relatively eutrophicated (Lauringson et al., 2012), regular pulses of nutrient-rich waters of the adjacent Gulf of Riga occur (Kotta et al., 2008b), and the studied algae are able to take advantage of these high nutrient events and store nutrients for extensive periods of time (Wallenti-

nus, 1984; Indergaard and Knutsen, 1990). Thus, the generic density-dependent effects and better performance of *F. lumbricalis* observed in this experiment are most likely associated with the light limitation of the red algae (this study; Kotta et al., 2008b). At low and medium densities *C. truncatus* filtered many times more light than the *F. lumbricalis* canopy of similar density (Fig. 4). It is therefore expected that negative growth rates, i.e. the process by which individuals in crowded and even-aged plant stands progressively die as a result of competition for light (Weller, 1987), is more likely for *C. truncatus* dominated red algal communities.

Difference in the arrangement of algal species within canopy may also explain the elevated growth of mixed communities compared to monospecific communities. Our observations clearly showed that mixed communities filtered out less light than their monospecific counterparts of the same density; thus, the light limitation is expected to be less severe in mixed communities compared to monospecific communities. As such, our results suggest that algal species that have relatively similar niches and have a high potential for interspecific competition actually benefit from the co-existence. Through modifying the community's physical structure, the algal mixture indirectly alters the physiological performance of both *F. lumbricalis* and *C. truncatus*, which therefore results in an elevated community productivity.

## 5. CONCLUSIONS

Our experimental observations on the loose-lying red macroalgal community supported the hypotheses that (1) algal growth is inversely related to their density as light limitation increases with algal density and that (2) algal growth is higher in mixed communities than in monospecific stands due to improved light conditions within mixed communities.

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## Kas kinnitumata punavetikate *Furcellaria lumbricalis* ja *Coccotylus truncatus* kasvukiirus sõltub nende tihedusest ning osakaalust koosluses?

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Väinamere põhja katab Euroopa meredes haruldane kinnitumata vetikakooslus, mille moodustavad peamiselt kaks punavetikaliiki: *Furcellaria lumbricalis* ja *Coccotylus truncatus*. Punavetikakooslus hõlmab Kassari lahe savi-liivastel põhjadel umbes 200 km<sup>2</sup> ala. Agariku *F. lumbricalis* kinnitumata vorm on ainsaks tõenduslikku tähtsust omavaks vetikaliigiks Läänemeres.

Uurimise eesmärgiks oli hinnata koosluse kasvutiheduse, punavetikate *F. lumbricalis* ja *C. truncatus* osakaalu ning nende tegurite koosmõju punavetikate kasvukiirusele. Välieksperimentide tulemusena selgus, et punavetikate kasvukiirus langeb märkimisväärselt koosluse tiheduse kasvades (0,010 g cm<sup>-3</sup> vrd 0,025 g cm<sup>-3</sup> ja 0,050 g cm<sup>-3</sup>). Üheliigiliste kooslustega võrreldes oli mõlema vetikaliigi kasvukiirus segakooslustes suurem. Samas mõjutas

punavetikate kasvukiirust ka nende osakaal koosluses: mõlema liigi puhul mõõdeti suurimad kasvukiiruse väärtused eksperimentides, kus nende suhteline osakaal punavetikakoosluses oli väike (25% vrd 50% ja 75%).

Vaadeldud erinevused punavetikate *F. lumbricalis* ja *C. truncatus* kasvukiiruses on tingitud peamiselt valguskliima eripärast erineva kolmemõõtmelise struktuuri ning eriliigilise koosseisuga kooslustes. Meie tulemustest selgus, et sama tiheduse juures oli valguse kasutamine efektiivsem segakooslustes. Ehkki kooselu samades ökoloogilistes tingimustes peaks üldjuhul viima liikidevahelise konkurentsini, saavad uuritud punavetikad kooseksisteerimisest hoopis kasu. Modifitseerides koosluse füüsilist struktuuri, tõstab punavetikate segakooslus kaudselt sealsete dominantide *F. lumbricalis* ja *C. truncatus* fotosünteetilist aktiivsust, mis omakorda viib punavetikakoosluse produktiivsuse tõusule.