Density dependent growth of the red algae *Furcellaria lumbricalis* and *Coccotylus truncatus* in the West Estonian Archipelago Sea, northern Baltic Sea*

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Abstract

In an in situ experiment we evaluated the growth of the red algae *Furcellaria lumbricalis* and *Coccotylus truncatus* in the Archipelago Sea. The results showed

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that the growth rates of both species were similar but that growth decreased with increasing algal coverage. The effects were more pronounced for *C. truncatus* than for *F. lumbricalis.* Economic analyses aiming to establish sustainable harvesting limits for *F. lumbricalis* in the study area should take account of the density dependent growth of these red algae.

1. Introduction

Competition has been recognised as one of the most important factors structuring macroalgal communities worldwide (Cousens & Hutchings 1983, Santelices & Ojeda 1984, Reed et al. 1991, Engkvist et al. 2004). Nevertheless, competitive interactions among marine macroalgae are little understood, and competitive ability is often estimated from plant sizes (e.g. Lobban & Harrison 2000). Only a few studies on exploitative competition between seaweeds have been carried out in the laboratory (Russel & Fielding 1974, Enright 1979) and even fewer under field conditions (Dudgeon et al. 1999, Kim 2002, Piazzi & Ceccherelli 2002).

Furcellaria lumbricalis (Hudson) J. V. Lamouroux is an abundant member of the marine flora in the colder waters of the North Atlantic and Arctic Oceans and is one of the few rhodophytes to flourish in the brackish Baltic Sea (Bird et al. 1991). The sheltered habitats of the Baltic Sea are occupied by the loose-lying form of *F. lumbricalis*; this community is best developed in the West Estonian Archipelago Sea (Martin 2000), where an extensive part of the archipelago is covered by drifting mats of *F. lumbricalis* and *Coccotylus truncatus* (Pallas) M. J. Wynne and J. N. Heine (Martin 2000). *F. lumbricalis* is the only economically important red algal species in the Baltic Sea and has been exploited in the study area since the 1960s. Besides its economic value, the loose-lying macroalgae enhance the diversity of the macroinvertebrates by offering a secondary substrate for several true hard-bottom species (Kotta & Orav 2001, Orav-Kotta & Kotta 2004, Lauringson & Kotta 2006).

For commercial and aesthetic reasons it is important to understand which variables contribute to the growth rate of both red algal species. In comparison with other macroalgae, the growth rates of *F. lumbricalis* and *C. truncatus* are low (Austin 1960a, Bird et al. 1979, Martin et al. 2006). The growth of these species in Western Europe is highest between February and June (Austin 1960b) and in the northern Baltic Sea between June and August (Blinova 1977, Martin et al. 2006). The delayed seasonal growth in our study area is due to the persistence of temperatures around 0°C until April–May (Kotta et al. 2008). Growth of these red algal species is optimum between 10 and 15°C (Bird et al. 1979, Rueness & Tanager

1984), and such temperatures prevail in the West Estonian Archipelago Sea in summer (Kotta et al. 2008).

The water in the Archipelago Sea is very turbid (Kotta et al. 2008) and the availability of light probably plays a crucial role in regulating the growth of red algae (Field et al. 1998). Although the loose-lying red algae are well adapted to reduced light conditions (Paalme 1994, Martin et al. 2006), the ambient light conditions in the Archipelago Sea are probably suboptimal for their growth, especially in thick algal mats. We therefore predict (a) that the growth of *F. lumbricalis* and *C. truncatus* is inversely related to their density and (b) that, as a result of similar niche selection (Martin et al. 2006), these red algal species have similar growth rates.

In view of the above, the aims of the study were to experimentally (1) evaluate the growth rates of *F. lumbricalis* and *C. truncatus* in the summer season and (2) estimate whether algal density modifies their growth rates. The experiment enabled us to find out whether density dependent growth regulates the populations of these economically important red algal species, and thus to provide a better basis for future resource management in the study area.

2. Material and methods

The West Estonian Archipelago Sea is a hydrodynamically very active water basin and is often separated from adjacent basins by sub-fronts. The salinity varies between 6 and 7 PSU. The region is periodically influenced by nutrient-rich water flowing in from the Gulf of Riga; hence, the state of the Gulf plays a significant role in the development of benthic communities in the West Estonian Archipelago Sea (Kotta et al. 2007). Sand and sandy clay substrates prevail in the study area. Drifting mats of *Furcellaria lumbricalis* and *Coccotylus truncatus* cover soft sediments at depths between 5 and 9 m, the community being maintained by the prevailing circular currents and the ring of islets that surround the area (Martin 2000).

Freshly collected *F. lumbricalis* and *C. truncatus* were incubated in nylon mesh bags (with plastic frame inside; diameter 5.5 cm, height 20 cm, 1 mm mesh size) (Martin et al. 2006) at 5 m depth from 31.05.2005 to 18.07.2005 (58.72°N, 23.10°E) (Table 1). Algae were deployed in densities of 5, 10, 15 and 20 mg cm^{-3} replicated five times. Algal densities represented realistic values in field conditions. Our design provided for normal water exchange between the algae and their surroundings, but without the algae moving around in the bag in sympathy with water movements (Figure 1).

Prior to the experiment, the wet weight of algae and the ratio of wet to dry weight of algae were determined. At the end of the incubation period the dry weight of the remaining algal material was measured. The relative

Table 1. Summary table of experimental treatments and levels

Red algal species	Density [mg cm^{-3}]
Furcellaria lumbricalis	5
Furcellaria lumbricalis	10
Furcellaria lumbricalis	15
Furcellaria lumbricalis	20
Coccotylus truncatus	5
Coccotylus truncatus	10
Coccotylus truncatus	15
Coccotylus truncatus	20

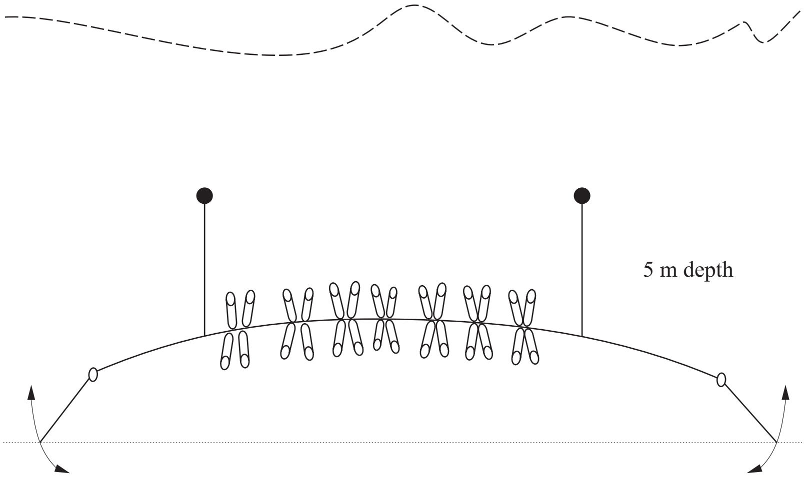

Figure 1. Experimental design

daily growth rates of both species of algae (DGR) were calculated using the equation

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

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

During deployment, the irradiance above and below the algal canopy was measured using a calibrated spherical quantum sensor connected to a data logger (ultraminiature logger for light intensity by Alec Electronics). When ordered at increasing densities, the respective algal treatments reduced light irradiance on average by factors of 2.1, 2.3, 2.7 and 3.2.

Two-way-analysis of variance (ANOVA) was performed to separate the effects of the two algal species and algal densities (5, 10, 15 or 20 mg cm^{-3}) on DGR. Bartlett's test was carried out prior to the analyses: the results confirmed the assumption of homoscedasticity. The post-hoc Bonferroni test was used to analyse which treatment levels were statistically different from each other (Sokal & Rohlf 1981).

3. Results

The growth of *Furcellaria lumbricalis* and *Coccotylus truncatus* decreased significantly with increasing algal densities (Table 2: two-way-ANOVA, effect of density, $F = 14.24$, $P < 0.001$). The effects were stronger for *C. truncatus* than for *F. lumbricalis*, as shown by the higher significance in differences between density treatment levels (post-hoc Bonferroni test: *C. truncatus* $p < 0.001$, *F. lumbricalis* $p < 0.05$).

Table 2. Summary of the two-way ANOVA analysis of the effect of algal species and density on the growth of *Furcellaria lumbricalis* and *Coccotylus truncatus* (relative daily growth rates, %). Significant effects are indicated in bold. The abbreviations denote the following: SS – Sum of Squares, DF – Degrees of Freedom, MS – Mean Square, F – F-statistics, P – Significance Level

Effect	SS	DF	MS	F	P
density	**1.203**	**3**	**0.401**	**14.24**	**< 0.001**
algal species	0.048	1	0.048	1.72	0.195
density × algal species	0.147	3	0.049	1.74	0.169

The growth rates of *C. truncatus* and *F. lumbricalis* were similar (two-way-ANOVA, effect of algal species, $F = 1.72$, $P > 0.05$). The effect of density was consistent as the interaction term between density and algal species was not significant (two-way-ANOVA, interactive effect of density × algal species, $F = 1.74$, $P > 0.05$) (Figure 2).

4. Discussion

The results of this experiment demonstrated that the growth rates of *Furcellaria lumbricalis* and *Coccotylus truncatus* were density dependent and were significantly higher at lower densities. Light and nutrients are traditionally considered to be the most important factors regulating macroalgal communities (Field et al. 1998). To date, however, no studies have demonstrated that *F. lumbricalis* is nutrient-limited. The species may conserve nutrients for periods of depletion and may thus escape nutrient limitation in late spring and summer (Indergaard & Knutsen 1990). Thus, the mechanism governing the interactions we observed is probably light limitation, as lower growth rates corresponded to poorer light conditions.

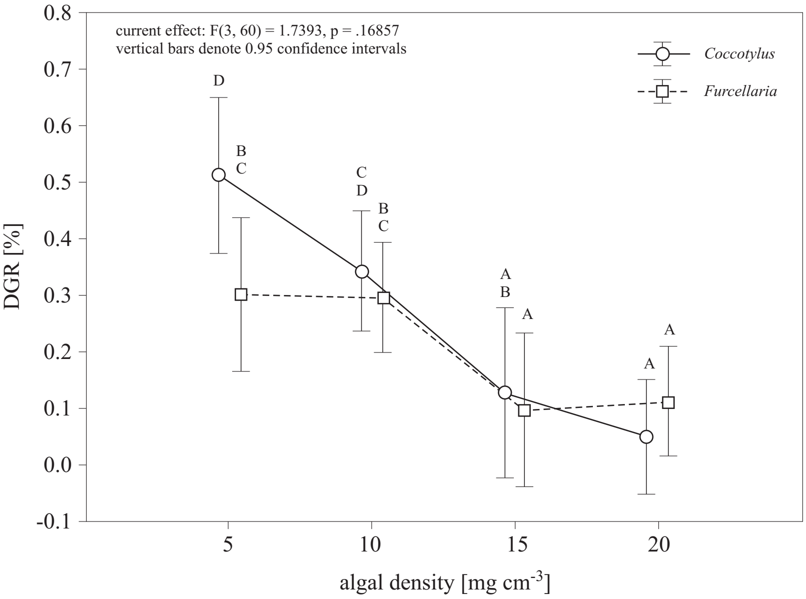

Figure 2. The relative daily growth rates of *Furcellaria lumbricalis* and *Coccotylus truncatus* at different density levels. The letters indicate homogeneous groups obtained from the post-hoc Bonferroni test of two-way ANOVA analysis

This concurs with an earlier assumption that it is primarily light that controls the growth and distribution of *F. lumbricalis* in nature (King & Schramm 1976, Bidwell & McLachlan 1985). Similarly, Wallentinius (1978) showed that the production rate of *F. lumbricalis* decreased with depth. Red algae are well adapted to reduced light conditions, as is demonstrated by their rapid light saturation at low quantum intensities as compared to other macroalgal species in the study area (Paalme 1994). Nevertheless, the light conditions are often suboptimal for red algal growth, especially in thick algal mats (Martin et al. 2006).

We predicted that *F. lumbricalis* and *C. truncatus* would have similar growth rates. This prediction was fulfilled, as we observed a consistent effect of density on growth rate regardless of species, and the combined effect of algal density and species was not statistically significant. This is in agreement with earlier observations that under similar light regimes the photosynthetic production of these red algal species is similar (Martin et al. 2006).

To conclude, density dependent interactions are important for the growth of these red algae, and their growth rates do not vary among species in the West Estonian Archipelago Sea. These results have important practical implications. Firstly, they suggest that the studied red algae are very resilient, and even when subjected to strong harvesting pressure they are capable of regaining their natural biomasses within one productive season (at low densities, red algae can almost double their biomass; see also Figure 2 for the growth rates). Secondly, despite similar growth rates, intensive harvesting may actually change the dominance structure of the red algae. *C. truncatus* has slightly finer filaments than *F. lumbricalis.* Thus, given identical biomasses, the former exhibits lower densities and higher coverages than the latter. At low stock densities, therefore, *C. truncatus* is expected to cover wider areas, spread more rapidly and regain its natural biomass faster than *F. lumbricalis.* Based on the above, future economic analyses aiming to establish sustainable harvesting limits should take account of the density dependent growth of these red algae.

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