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RESEARCH ARTICLE

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# Intraspecific competition in *Fucus serratus* and *F. evanescens* (Phaeophyceae: Fucales) germlings: effects of settlement density, nutrient concentration, and temperature

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**Abstract** Survival and growth of early post-settlement stages are critical for the development of seaweed populations. Fucoid germlings commonly settle in dense monospecific aggregates, where intraspecific competition and environmental variables (e.g. nutrient concentration and temperature) may affect survival and growth. Using factorial experiments, we determined the effects of settlement density (~10, ~50 and ~250 germlings $cm^{-2}$), nutrient enrichment (from ~10 to ~40 µM N and from ~0.5 to ~2.5 µM P), and temperature (7°C and 17°C) on *Fucus serratus* and *F. evanescens* germlings in laboratory cultures over 3 months. Settlement density, nutrient concentration and temperature interactively affected growth of germlings, and the magnitude of this interaction varied between the two species. This represents the first record of such factorial interactions in *Fucus* spp. germlings. Intraspecific competition, estimated as the relative reduction in germling growth and survival from low to high densities, increased with decreasing nutrient concentration and increasing temperature in both species. While temperature and nutrient concentration had little effect on germling size distributions, size inequality and skewness generally increased with germling density, indicating that a few large individuals gained dominance and suppressed many smaller ones at high density. Self-thinning increased with settlement density and depended on nutrient concentration and species at high density. At high density, self-thinning increased with decreasing nutrient levels in *F. evanescens*, but not in *F. serratus*. At low density, nutrient enrichment increased germling growth in *F. evanescens*, but not in *F. serratus*, whereas growth in both species was stimulated by nutrient enrichment at higher densities. These results suggest that germling growth and self-thinning are more sensitive to variation in nutrient concentration in *F. evanescens* than in *F. serratus*. The potential implications of our findings for the understanding of eutrophication-related abundance changes in both species in southern Norway are discussed.

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## Introduction

Early stages of substrate colonisation usually represent a bottleneck in the development of seaweed populations, as germlings are generally more susceptible to physical and biological stresses than adults (Brawley and Johnson 1991; Lotze et al. 2001; Worm et al. 2001). Fucoids (Phaeophyceae: Fucales) are the dominant intertidal seaweeds on rocky shores along northern Atlantic coasts, and their persistence depends on the survival and growth of early post-settlement stages (Vadas et al. 1992). Fucoid germlings often settle in dense monospecific stands, close to the parent plants (Kendrick 1994; Creed et al. 1996a; Arrontes 2002), where growth and survival are likely affected by intraspecific competition. For some seaweeds, but most notably for terrestrial plants, intraspecific competition has been investigated through density-manipulation experiments. Three major effects of intraspecific competition have been identified in dense plant stands (Yoda et al. 1963; Silvertown and Charlesworth 2001). At high density the mean size of plants is reduced ("competition–density effect"), the probability of survival is reduced ("self-thinning"), and, as a consequence of these two processes, the size structure of individuals within stands is altered compared with low-density stands. Although self-thinning and size structure have been described for fucoids (Creed 1995; Creed et al. 1998; Arenas and Fernández 2000; Arenas et al. 2002; Karez 2003), density dynamics at the germling stage have not been studied as thoroughly (Creed et al. 1997; Choi 2001; Steen 2003).

Both positive (facilitation) and negative (competition) effects of density have been recorded in stands of fucoid seaweeds (positive: Hruby and Norton 1979; Ang and DeWreede 1992; Andrew and Viejo 1998; negative: Kendrick 1994; Creed et al. 1997, 1998). Density responses of germlings likely depends on growth conditions; observations of density facilitation have mainly been done in intertidal areas characterised by abiotic stress, where high density offers protection from stressful factors and outweighs the costs of competition (Bertness et al. 1999). The relationship between density and other factors regulating the development of fucoid germlings has been little explored. Along the coasts of southern Norway, the dominant low-shore fucoid *Fucus serratus* L. reproduces close to year round, while another low-shore fucoid, the introduced *Fucus evanescens* C. Agardh, has a more defined reproductive season in spring and early summer (Rueness 1998; Steen and Rueness 2004). Because of the extended reproduction of these species, their germlings encounter large variations in environmental factors (e.g. temperature and nutrient concentration), which may interactively affect density dynamics, growth and survival.

The objective of the present study was to examine interactive effects of settlement density, nutrient concentration, and temperature on growth and survival of *F. serratus* and *F. evanescens* germlings, using factorial laboratory experiments. We predicted that survival and growth of germlings would be inversely related to settlement density, and that the intensity of competition–density effects, self-thinning and changes in size structure would depend on nutrient concentration and temperature. Increased competition for nutrients would be expected when nutrients are in limited supply, while less resource consumption would likely reduce competition at temperatures sub-optimal for germling growth. We compare the responses of the two species and discuss the possible ecological implications for the larger spatial context.

## Materials and methods

### Experimental design

Reproductive plants were collected near Langesund (58°59′N; 9°45′E), on the Skagerrak coast of Norway, in November 1998 (*Fucus serratus*) and March 2000 (*F. evanescens*). In the laboratory, receptacles were excised and repeatedly washed in cold tap water to remove epiphytes. Gamete release and zygote suspensions were achieved using standard techniques for fucoids (Quatrano 1980). The initial concentration of zygotes was determined using a Palmer–Maloney chamber under a stereomicroscope. Density gradients of germlings were made by serially diluting the initial zygote suspensions three times by a factor of five and transferring the resuspensions to three equally sized plastic chambers, each containing 35 plexi-slides (9 cm$^2$) on the bottom. The chambers were then placed at 12°C for settlement to proceed. The incubation temperature of 12°C was considered ideal, because both species reproduce at this temperature and because acclimation procedures are less extensive, as 12°C is equally distant from experimental temperatures (see below). After 5 days of incubation, 16 slides were chosen from each settlement chamber, based on criteria such as closeness to desired density levels (10, 50 and 250 germlings cm$^{-2}$) and non-patchy distribution of germlings, and each slide was then placed in a separate growth chamber (4 cm high). These settlement densities are below maximum values recorded for fucoid species in the field (up to 900 germlings cm$^{-2}$ for *F. serratus*; Creed et al. 1996a), but are realistic given the natural variations along the shoreline (Kendrick 1994). The slides were covered with 3 cm of growth medium, which was changed twice a week, and were kept under a 16 h light:8 h dark cycle, at 50 µE m$^{-2}$ s$^{-1}$. Before each medium renewal, slides were carefully sprayed with sterile seawater to remove necromass and dross. Germanium dioxide (0.2 mg l$^{-1}$, a concentration suggested by Markham and Hagmeier 1982) and penicillin (2 mg l$^{-1}$) were added to the cultures to reduce growth of diatoms and prokaryotes, respectively.

A factorial design was used to test for the interaction of temperature (two levels: 7°C and 17°C), nutrient concentration (two levels; see below), and settlement density (three levels; see above). These temperature levels resemble spring (7°C) and summer (17°C) water temperatures along Skagerrak shores and cover most of the temperature range during the reproductive season for *F. serratus* and *F. evanescens*. Four replicate slides were used for each species at each treatment (2 species×12 treatments×4 replicates = 96 slides in total). A low nutrient level was obtained from seawater collected from the Oslofjord at a depth of 1 m, with a salinity of 25‰ and nutrient concentration of ~10 µM N (ammonia + nitrate) and ~0.5 µM P (phosphate). High nutrient concentration was obtained by enriching other samples of similar seawater with 32 µM N (with nitrate:ammonia added in a 1:1 ratio) and 2 µM P (phosphate), which is comparable to nutrient concentrations in eutrophic fjord systems (Kristiansen and Paasche 1982).

### Measurements

The experimental slides were non-destructively sampled after 5, 31, 52, 71 and 90 days (± 1) of cultivation. Density was measured by counting germlings divided by area. At low density, all germlings on a slide were counted, while, at higher densities, germlings in four subsections (with areas ranging from 0.27 to 1.1 cm$^2$, depending on germling density) were counted. To keep potential edge effects to a minimum and equal between slides, the positions of the sampled subsections were kept as similar as possible between slides and sampling dates, always at least 3 mm away from edges. Survival was estimated as the proportional difference in number of germlings between the date of sampling and start of experiment (day 5). In each sampling session, germlings were carefully forced down in a plane with a microscope slide and a section of each slide was photographed using a video camera through a stereomicroscope. The images were digitised, and the surface area projections of five to ten germlings (henceforth referred to as germling area) were measured in each image using a software tool (Scion Image, available from Scion Corporation, http://www.scioncorp.com). In images containing more than ten germlings, the individuals to be measured were selected along a diagonal transect always starting from the same corner. Although some individuals overlapped in the images of high-density slides towards the end of the experiment, germlings were translucent enough for the outlines of underlying individuals to be recognised. After 90 days of cultivation, slides were briefly soaked in fresh water to remove salt. Germlings were then shaved off the slides, dried at 50°C and weighed to the nearest 0.1 mg. Correlations between biomass (total dry mass of germlings per slide) and bioarea (mean germling area×number of germlings per slide) were established for each species.

### Data analysis

#### *Intraspecific density dynamics*

Competition is commonly measured through indices comparing the performance of individuals at different density levels (Grace 1995).

Because performance of individuals at low density, in particular, often varies with environmental conditions, it is more meaningful to assess the effects of competition on a relative, rather than absolute, basis (Grace 1995). We estimated relative competition–density (RCD) effects as the difference between the bioarea ($A_o$ = mean germling area×germling density) of a high-density culture and its potential "competition-free" bioarea [$A_p$ = mean germling area (at low density)×mean survival (at low density)×settlement density (at high density)] after the same period of growth:

$$\mathrm{RCD} = (A_o - A_p) \times X^{-1} \tag{1}$$

where $X$ is $A_o$, when $A_o$ is greater than $A_p$, and $A_p$, when $A_p$ is greater than $A_o$ (Markham and Chanway 1996). The RCD index integrates density effects on mean size and survival of germlings, and is a measure of the total intraspecific interaction intensity. Values of the RCD index range between −1 and 1, with negative values indicating competition and positive values indicating facilitation.

If competition becomes severe enough, death of the suppressed individuals will occur (self-thinning), which can be regarded as the ultimate manifestation of intraspecific competition (Morris 2003). Self-thinning was analysed using bi-logarithmic plots of standing biomass (in g $m^{-2}$) versus density (in germlings $m^{-2}$) through time. These units were chosen to enable comparisons with biomass–density relationships for other seaweeds and for terrestrial plants. During self-thinning, the biomass–density relationship approaches and follows a straight line with a negative slope, termed the "self-thinning line" (Weller 1987, 1989). In the present study, reduced major axis regression (RMA, a variant of model II regression) was used to calculate self-thinning lines, because both variables were random and subject to error (Sokal and Rohlf 1995). Although it is essential to exclude pre-crowding data points before fitting the lines, as their inclusion would tend to overestimate the steepness of the true self-thinning line, few good objective criteria exist to detect self-thinning (Westoby 1984; Lonsdale 1990; Bi and Turvey 1997). We only included data from the highest settlement density category and only from samplings after which significant competition–density effects (as described above) had been recorded on the previous sampling date, as competition–density effects generally precede self-thinning (Osawa and Sugita 1989).

Whereas the RCD index measures the total increase in competition intensity from low- to high-density cultures, the position of the self-thinning line can be used as a measure of intraspecific competition increase per biomass unit accumulated. In even-aged cultures of similar initial densities, flatter self-thinning slopes indicate higher competition intensity than steeper slopes, as more individuals die for every gram of biomass produced. When two self-thinning slopes are similar, a lower biomass range and intercept indicates a decreased tolerance to intraspecific competition, because less biomass accumulates before a certain amount of self-thinning occurs. When comparing self-thinning lines at different biomass ranges, one also has to consider that biomass increases more for every dead individual along a line positioned higher in the diagram due to the bi-logarithmic nature of the graph.

To describe variations in size distribution of germlings, Gini coefficients were calculated (Kokko et al. 1999). Gini coefficients characterise size inequality on a scale from 0 (total equality) to 1 (maximum inequality). To further explore variation in size structure between treatments at the end of the experiment, the size-frequency distributions at each treatment level are presented in histograms.

### *Statistics*

Four-way univariate analyses of variance (ANOVA) were performed to test for treatment effects on mean germling area and survival. The independent variables (settlement density, nutrient concentration, temperature, and species) were considered orthogonal and fixed. The magnitude of main effects and interactions was calculated as the percent variance explained, using the omega-squared ($\omega^2$) measure as recommended for fixed-factor models (Howell 1992). The direction of treatment effects and interactions was interpreted graphically. Lower-order ANOVAs were performed to test for effects within subgroups of treatments, and Student's *t*-tests were used for post hoc comparison of treatment pairs. The validity of using *t*-tests after ANOVAs follows the suggestions of Carmer and Walker (1982), Hurlbert (1990), Mead (1991) and Soto and Hurlbert (1991).

Probability levels (*P*-values) were estimated by resampling and randomly redistributing the data over treatment levels and, for each run, recalculating the test statistic (*F*-ratio in the case of ANOVAs, *t*-value in the case of *t*-tests), as described in Crowley (1992). The *P*-value is given by the number of times the resampled test statistic proved to be at least as extreme as the original test statistic, divided by the total number of resamplings (1,000). To ensure homogeneity of variances, as required for resampling methods involving randomisation of data across samples, germling area data were logarithmically transformed and survival ratios were angular (arcsine–square root)-transformed.

Confidence intervals for means, Gini coefficients, RCD indices and self-thinning lines were calculated using the bootstrap percentile method (Dixon 2001). In this method, the 2.5 and 97.5 percentiles of the bootstrapped (resampled with replacement within each level of variation) distribution are used as the limits of a 95% confidence interval, which correspond to the 25th and 975th largest values when 1,000 resamplings are run. In the cases of germling area measurements, with variation components within and between slides, multistage resamplings were performed with the lower level (slide) nested at the higher level (treatment). Compared with conventional parametric procedures, based on the assumption of normal data distributions, resampling procedures will be independent of the underlying distribution of data as the statistical estimates are produced by taking samples directly from the available data. Resampling methods are thus more flexible and will provide more reliable statistical estimates than conventional normality-requiring procedures, especially in cases of small samples, where the shapes of data distributions are indeterminable (Crowley 1992). All computations were done in Microsoft Excel 97 for Windows, and the resamplings were run using an Excel macro, available from Resampling Stats (http://www.resample.com).

## Results

### Checking the methods and treatment efficacy

As a result of the dilution procedure, density of settled zygotes fell into three significantly distinct categories for each species (*t*-tests, $P$ always $<0.05$, Fig. 1). Mean (±95% confidence limits) settlement densities were 9.0 (±0.3), 43.5 (±2.0) and 215 (±8.8) germlings $cm^{-2}$ in *Fucus serratus*, and 11.7 (±0.4), 49.0 (±2.4) and 205 (±6.8) germlings $cm^{-2}$ in *F. evanescens*. A four-way ANOVA (Table 1) revealed that there was a significant difference in settlement density between the two species [$F_{\mathrm{Species}}(1,72) = 37.7$, $P < 0.001$], and that this interspecific difference varied between density categories [$F_{\mathrm{Species \times Density}}(2,72) = 24.0$, $P < 0.001$]. Settlement density of *F. evanescens* germlings was significantly higher than that of *F. serratus* at the two lowest density categories (*t*-tests, $P < 0.05$ in both cases), whereas no significant difference existed between the two species in the high-settlement-density category (*t*-test, $P = 0.12$). Compared with the large intraspecific differences between density categories (~400%), the interspecific differences in settlement

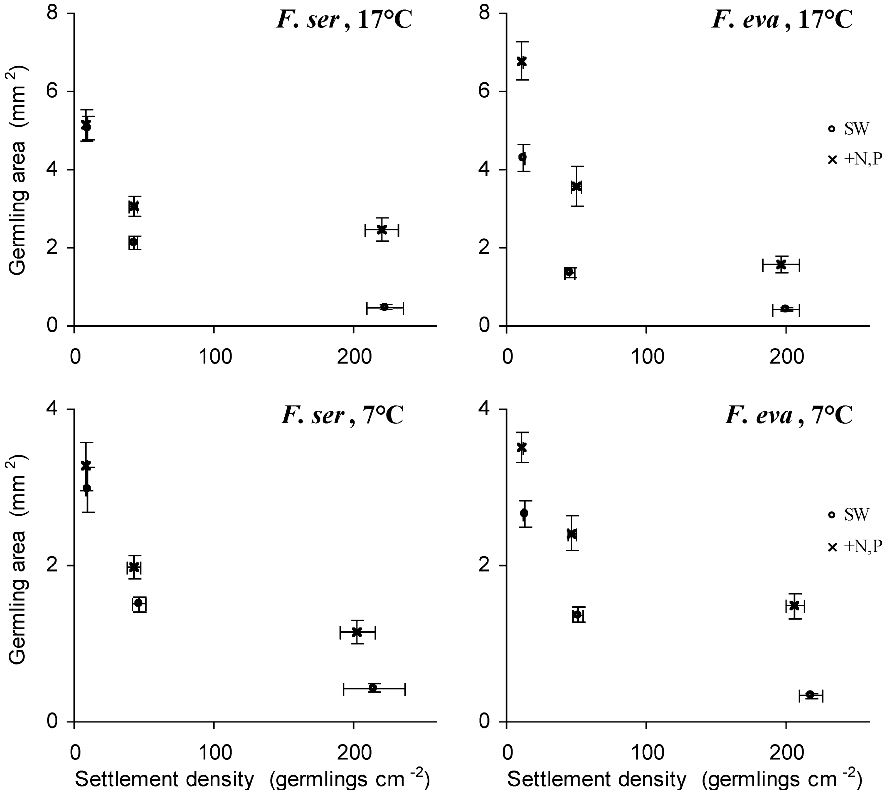

**Fig. 1** *Fucus serratus* (*F. ser.*) and *F. evanescens* (*F. eva.*). Mean area of germlings as a function of settlement density after 90 days of cultivation at 7°C and 17°C in seawater (*SW*) and N-P-enriched seawater (+*N,P*). Error bars denote 95% confidence limits. Note the difference in scale between the upper and lower panels

**Table 1** *Fucus serratus* and *F.evanescens*. *F*-ratios from four-way ANOVAs of differences in settlement density across treatments, and treatment effects on mean germling area and survival after 90 days of cultivation. The magnitude of explained variance ($\omega^2$, in percent) for significant treatment effects ($P < 0.05$) is shown *in parentheses*

| Source of variation | *df* | Settlement density | Area | Survival |
|---|---|---|---|---|
| Species (S) | 1 | 37.71 (< 1) | 3.097 | 2.652 |
| Temperature (T) | 1 | 3.220 | 472.3 (7) | 14.08 (5) |
| Nutrients (N) | 1 | 2.311 | 1,022 | 22.75 (9) |
| Density (D) | 2 | 10,088 (99) | 2,133 | 37.10 (30) |
| S×T | 1 | 1.864 | 12.41 | 6.832 (2) |
| S×N | 1 | 0.157 | 51.30 | 11.29 (4) |
| T×N | 1 | 3.133 | 40.87 | 0.926 |
| S×D | 2 | 24.09 (< 1) | 4.245 | 3.802 (2) |
| T×D | 2 | 0.673 | 48.61 | 2.775 |
| N×D | 2 | 0.108 | 114.5 | 2.412 |
| S×T×N | 1 | 0.404 | 0.185 | 0.849 |
| S×T×D | 2 | 1.553 | 10.74 | 0.346 |
| S×N×D | 2 | 0.293 | 17.64 | 2.919 |
| T×N×D | 2 | 1.175 | 4.105 | 1.537 |
| S×T×N×D | 2 | 0.306 | 23.67 | 2.667 |
| Residual | 72 | (< 1) | (2) | (40) |

density in the two lowest density categories (~20%) were assumed to have negligible effects on responses, and ignored whenever treatment effects were compared across species. There was no significant difference in intraspecific settlement density among levels of the two factors to be assigned subsequently, temperature and nutrient concentration (Table 1, $P > 0.05$ for all main and interaction terms involving temperature and nutrient concentration).

## Germling area and survival

Treatment effects were most pronounced after 90 days of cultivation, so those are the only recordings shown in tables and graphics. After 90 days, there was a significant four-way interaction effect of temperature, nutrient concentration, settlement density, and species on mean germling area (Table 1). The relative magnitude of treatment effects ($\omega^2$) showed that settlement density explained two-thirds of the variation in germling area (Table 1). In both species, germling area was negatively related to settlement density at all temperature and nutrient levels (Fig. 1). Increasing temperature and nutrient concentration generally increased germling area; the extent of this stimulation depended on settlement density and species (Fig. 1). At the low settlement density, germling area was significantly stimulated by nutrient enrichment in *F. evanescens* [Fig. 1; *t*-tests, $P < 0.05$ (at 7°C) and $P < 0.05$ (at 17°C)], but not in *F. serratus* [Fig. 1; *t*-tests, $P = 0.36$ (at 7°C) and $P = 0.71$ (at 17°C)]. At higher settlement densities, germling area was significantly stimulated by nutrient enrichment in both species at both temperatures tested (Fig. 1; *t*-tests, *P* always < 0.05).

Temperature, nutrient concentration, and settlement density had significant effects on germling survival after

90 days of cultivation, and the magnitude of these effects depended on species (Table 1). In both species, germling survival was negatively related to settlement density (Fig. 2). In *F. serratus*, the negative effect of density on germling survival increased with increasing temperature and nutrient concentration [Fig. 2; three-way ANOVA, $F_{\mathrm{Temperature\times Nutrients\times Density}}(2,36)=3.3$, $P<0.05$]. In the high-density, nutrient-enriched cultures, germling survival was significantly lower in *F. serratus* than in *F. evanescens* at 17°C (Fig. 2; $t$-test, $P<0.05$), but not at 7°C (Fig. 2; $t$-test, $P=0.78$). At lower settlement densities, survival of germlings differed little between species, temperature, and nutrient treatments ($t$-tests, $P$ always $>0.05$).

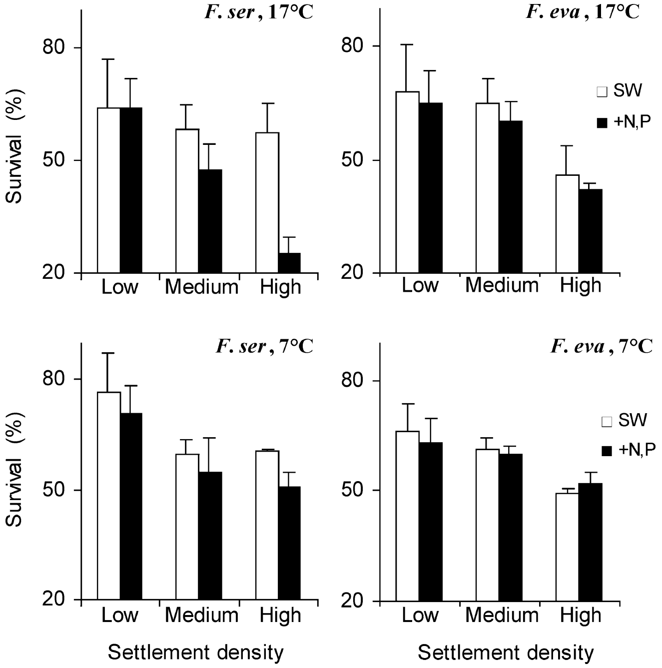

**Fig. 2** *Fucus serratus* (*F. ser.*) and *F. evanescens* (*F. eva.*). Mean survival of germlings as a function of settlement density after 90 days of cultivation at 7°C and 17°C in seawater (*SW*) and N-P-enriched seawater (*+N,P*). Error bars denote upper 95% confidence limits (*low*, *medium* and *high* 10, 50 and 250 germlings cm$^{-2}$, respectively)

## Intraspecific density dynamics

In both species significant relative intraspecific competition effects (i.e. negative 95% confidence intervals of the RCD index) were observed after 31 days of cultivation, and the competition intensified until termination of the experiments, after 90 days (Table 2). To keep the presentation simple, estimates of relative intraspecific competition made after 52 and 71 days were omitted from Table 2, as these values always ranged between the estimates for days 31 and 90. Intraspecific competition generally increased (RCD index decreased) with increasing settlement density and temperature, and decreased (RCD index increased) with increasing nutrient concentration (Table 2). There were no significant differences in intraspecific competition effects between *F. evanescens* and *F. serratus*, as the 95% confidence intervals of the RCD index overlapped between species in all treatment combinations (Table 2).

Self-thinning increased with settlement density in both *F. evanescens* and *F. serratus*, as biomass–density trajectories became shallower over time (Fig. 3A, B). Only data points from the high-density cultures between 52 and 90 days were considered sufficiently crowded to be included in regressions (Fig. 3C, D), as significant intraspecific competition effects, presumed to precede self-thinning effects, were recorded in all these cultures after 31 days (Table 2). Although some of the high-density cultures had progressed further along the self-thinning line at 17°C than at 7°C, most pronounced in the nutrient-enriched *F. serratus* cultures, temperature had no significant effect on the slope and intercept of self-thinning lines, so this factor was pooled. Self-thinning patterns were influenced by nutrient concentration in the high-density cultures of both *F. serratus* and *F. evanescens*, but the species responded differently. At low nutrient levels, *F. evanescens* cultures had a significantly (disjunctive 95% confidence intervals) lower intercept and biomass range than in the enriched cultures, while self-thinning slopes did not differ significantly (slightly overlapping 95% confidence intervals) between nutrient levels (Fig. 3C). At the low nutrient level, the self-thinning line of *F. serratus* had a significantly steeper slope

**Table 2** *Fucus serratus* and *F.evanescens*. Mean relative competition–density index (±95% confidence limits) estimating the relative competition intensity (see "Materials and methods" for explanation) at medium (50 germlings cm$^{-2}$) and high (250 germlings cm$^{-2}$) settlement densities, after 31 and 90 days of cultivation at 7°C and 17°C in seawater (*SW*) and N-P-enriched seawater (*+N,P*)

| Cultivation period | Temp. | Medium settlement density | | | | High settlement density | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | SW | | +N,P | | SW | | +N,P | |
| | | *F.ser.* | *F.eva.* | *F.ser.* | *F.eva.* | *F.ser.* | *F.eva.* | *F.ser.* | *F.eva.* |
| 31 days | 17°C | −0.37±0.16 | −0.34±0.11 | −0.35±0.19 | −0.33±0.15 | −0.51±0.09 | −0.65±0.06 | −0.53±0.12 | −0.41±0.09 |
| | 7°C | −0.31±0.2 | −0.16±0.12 | −0.27±0.18 | −0.03±0.16 | −0.48±0.12 | −0.48±0.06 | −0.31±0.13 | −0.18±0.12 |
| 90 days | 17°C | −0.62±0.1 | −0.70±0.05 | −0.56±0.1 | −0.51±0.07 | −0.91±0.02 | −0.93±0.01 | −0.82±0.05 | −0.85±0.02 |
| | 7°C | −0.61±0.1 | −0.52±0.1 | −0.52±0.11 | −0.34±0.08 | −0.88±0.03 | −0.90±0.02 | −0.75±0.05 | −0.66±0.04 |

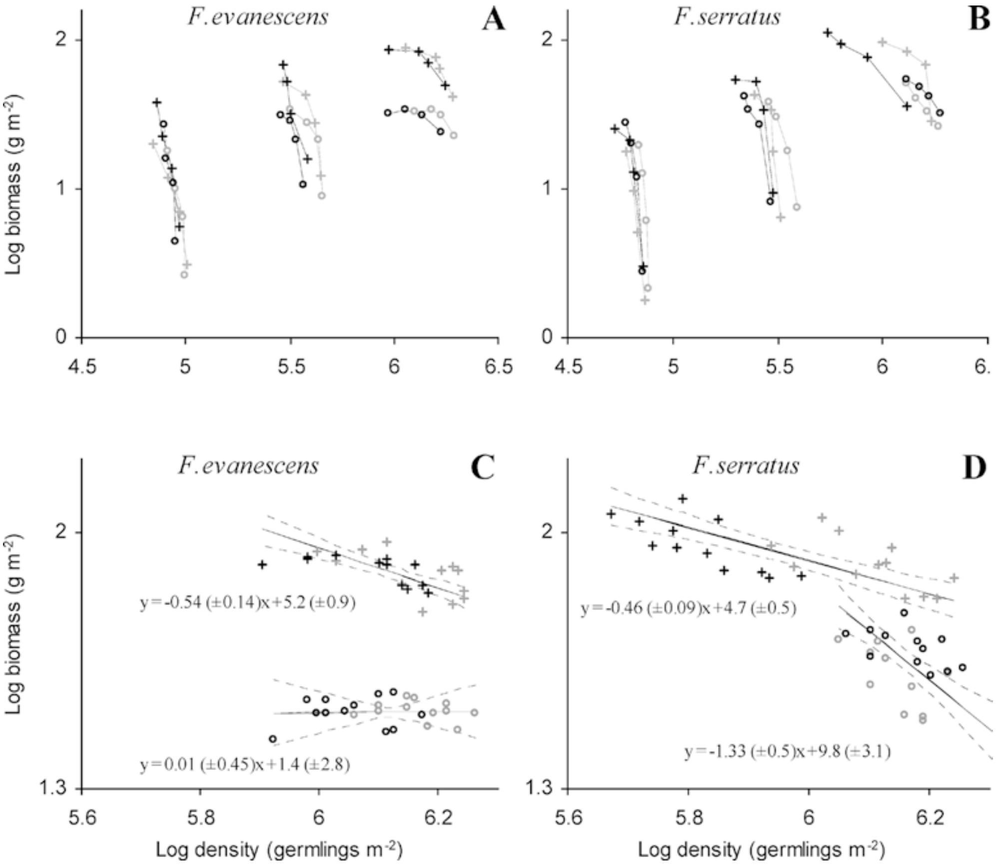

**Fig. 3** *Fucus evanescens* (**A**, **C**) and *F. serratus* (**B**, **D**). **A**, **B** Mean dynamic biomass–density trajectories from day 31 (lower end of trajectories) to day 90 (upper end of trajectories) in cultures cultivated at 7°C (*grey symbols*) and 17°C (*black symbols*), in seawater (*open circles*) and nutrient-enriched seawater (*crosses*). **C**, **D** Linear, reduced-major-axis-regressed self-thinning lines (±95% confidence limits) at high settlement density between days 52 and 90, with the temperature factor pooled. The 95% confidence limits for slopes and intercepts are shown, $n=24$

and higher intercept and occupied a lower biomass range than in the nutrient-enriched cultures (Fig. 3D). The self-thinning line in the high-density cultures of *F. evanescens* had a significantly shallower slope, intercept and biomass range than in *F. serratus* at the low nutrient level, whereas no significant interspecific difference in self-thinning line patterns was observed at the high nutrient level (Fig. 3C, D).

Five days after settlement, the size inequality (Gini coefficient) of germlings ranged between 0.06 and 0.10 and was independent of density in both species (Table 3). After 31 days, size inequality in most of the high-density treatments increased significantly, while size distributions changed little at low density. After 90 days, germling size distributions at low settlement density still appeared close to normal, whereas size distributions appeared more positively skewed and germling sizes more unequal at higher densities (Fig. 4; Table 3). Differences in germling size distributions between species, temperatures, and nutrient levels were relatively small apart from at medium density in *F. evanescens*, where germling size inequality increased twofold when temperature and nutrient concentration were jointly increased (Table 3).

**Table 3** *Fucus serratus* and *F.evanescens*. Mean Gini coefficients (±95% confidence limits) describing germling size inequality 5, 31 and 90 days after settlement under various density (*low*, *medium*and *high* 10, 50 and 250 germlings cm$^{-2}$, respectively) and temperature regimes in seawater (*SW*) and N-P-enriched seawater (+*N,P*)

| Age | Temp. | Nutrient level | *F.serratus* settlement density | | | *F.evanescens* settlement density | | |
|---|---|---|---|---|---|---|---|---|
| | | | Low | Medium | High | Low | Medium | High |
| 5 days | | | 0.08 ± 0.02 | 0.08 ± 0.01 | 0.1 ± 0.02 | 0.08 ± 0.01 | 0.06 ± 0.01 | 0.06 ± 0.01 |
| 31 days | 17°C | +N,P | 0.09 ± 0.02 | 0.11 ± 0.02 | 0.16 ± 0.03 | 0.08 ± 0.01 | 0.1 ± 0.02 | 0.11 ± 0.02 |
| | | SW | 0.08 ± 0.02 | 0.14 ± 0.02 | 0.18 ± 0.04 | 0.08 ± 0.02 | 0.12 ± 0.02 | 0.14 ± 0.03 |
| | 7°C | +N,P | 0.11 ± 0.04 | 0.1 ± 0.02 | 0.12 ± 0.02 | 0.07 ± 0.01 | 0.09 ± 0.02 | 0.11 ± 0.02 |
| | | SW | 0.1 ± 0.03 | 0.16 ± 0.03 | 0.18 ± 0.03 | 0.06 ± 0.01 | 0.12 ± 0.02 | 0.15 ± 0.03 |
| 90 days | 17°C | +N,P | 0.09 ± 0.02 | 0.16 ± 0.03 | 0.2 ± 0.04 | 0.1 ± 0.02 | 0.24 ± 0.04 | 0.23 ± 0.03 |
| | | SW | 0.07 ± 0.02 | 0.14 ± 0.02 | 0.22 ± 0.04 | 0.11 ± 0.03 | 0.15 ± 0.03 | 0.2 ± 0.03 |
| | 7°C | +N,P | 0.1 ± 0.03 | 0.12 ± 0.02 | 0.22 ± 0.04 | 0.08 ± 0.01 | 0.16 ± 0.02 | 0.19 ± 0.03 |
| | | SW | 0.12 ± 0.03 | 0.12 ± 0.03 | 0.18 ± 0.03 | 0.09 ± 0.02 | 0.12 ± 0.02 | 0.16 ± 0.03 |

## Discussion

We examined the interactive effects of settlement density, temperature, and nutrient concentration on the intraspecific competition, self-thinning, and size structure of *Fucus evanescens* and *F. serratus* germlings. Mean size and survival of germlings were negatively related to settlement density, likely due to competition, as resource (space, nutrients and light) availability per individual decreased with increasing density. For both species, significant intraspecific competition effects (relative reduction of growth and survival from low to high densities) were recorded after 1 month of cultivation, and increased over the following 2 months as individuals grew in size, likely consuming more resources. Intraspecific competition increased with decreasing nutrient concentration for both species. Nutrient competition among even-aged, conspecific germlings is probably

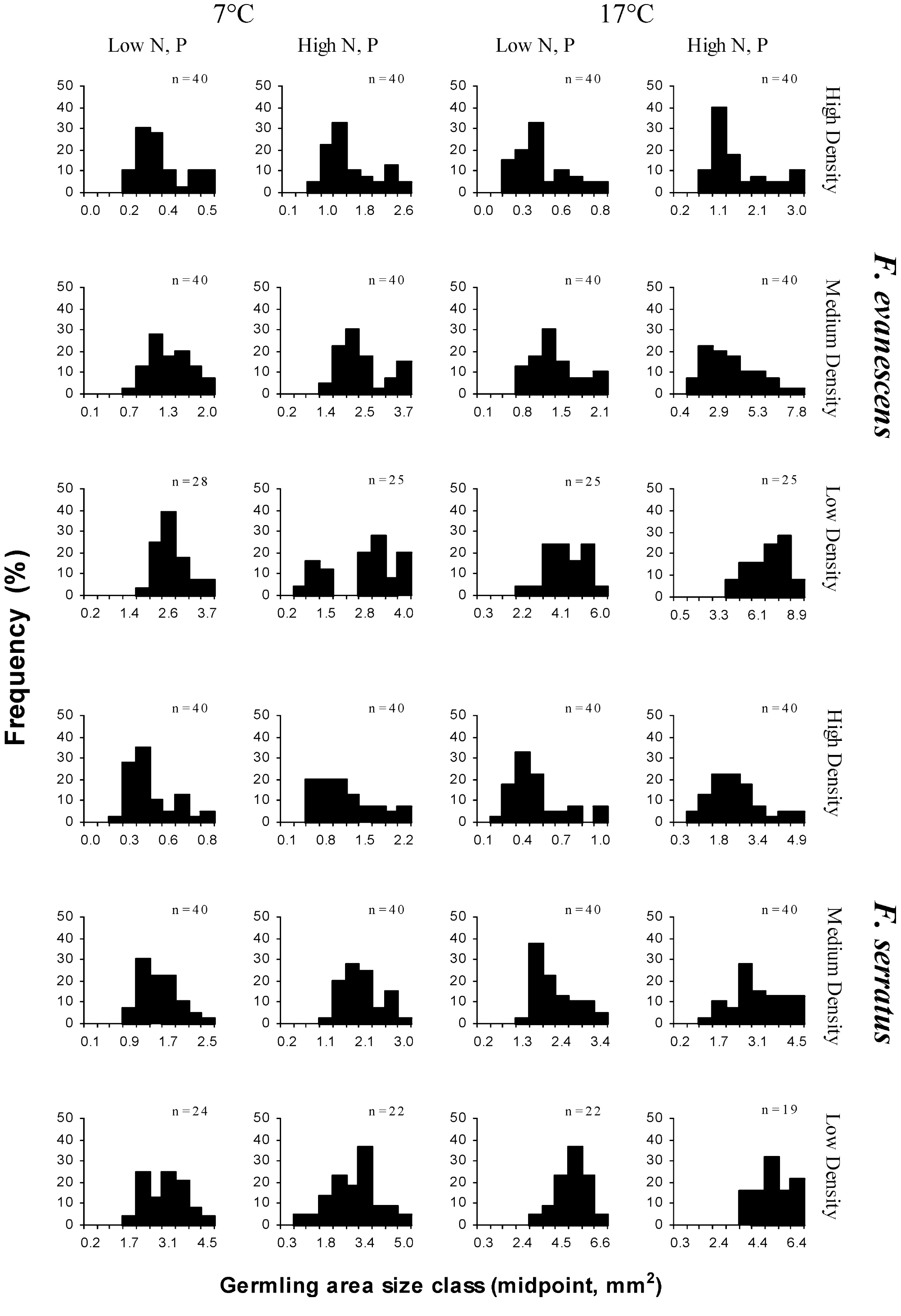

**Fig. 4** *Fucus evanescens* (*upper panels*) and *F. serratus* (*lower panels*). Size-frequency distributions of germlings, after 90 days of cultivation in different density, temperature, and nutrient regimes (see "Materials and methods for details on regimes)

more important than competition for light, as shading effects are low under thin layers of germlings (Creed et al. 1997). Beneath a canopy of adults, on the contrary, germlings could indeed be light limited (Reed 1990). The negative relationship between nutrient enrichment and intraspecific competition was more pronounced at 17°C than at 7°C, probably as a result of stronger interactions among the faster growing, and likely more resource-demanding, germlings at high temperature. These results represent, to the best of our knowledge, the first recordings of interactive effects of temperature, nutrient concentration, and settlement density on the growth and survival of *Fucus* spp. germlings, and agree with previous findings for germlings of the invasive fucoid *Sargassum muticum* (Yendo) Fensholt (Steen 2003).

As biomass accumulates and competition increases in a culture, self-thinning eventually occurs. In our study, the intensity of self-thinning increased with settlement density in both *F. evanescens* and *F. serratus*, as biomass–density slopes became shallower. This implies that, when biomass increases to a certain degree, mortality is higher at high than at low settlement densities. In the high-density *F. serratus* cultures, the self-thinning line had a steeper slope, higher intercept, and was positioned at a lower biomass range at the reduced nutrient level. The same phenomena have been reported for terrestrial plants when soil fertility was varied (Westoby 1984; Morris 2003) and are likely caused by a time lag in crowding-induced mortality due to lower growth and biomass accumulation rates when nutrients are scarce. In this case, nutrient enrichment may simply speed up the progression towards a common self-thinning line (Morris and Myerscough 1985). However, in the high-density *F. evanescens* cultures, reduced nutrient levels appeared to simultaneously decrease the slope (although 95% confidence limits of slopes overlapped slightly between nutrient levels), intercept, and biomass range of the self-thinning line. Reduced fertility levels have previously been shown to flatten self-thinning lines in dense stands of terrestrial plants (Morris 1999, 2002, 2003), which implies that mortality increases more per biomass unit accumulated as fertility levels decrease. In this case, nutrient enrichment appears to increase the competition ability of individuals, as a higher level of biomass packing is tolerated before a certain amount of self-thinning occurs. It is interesting to note that the results recorded in our high-density, nutrient-enriched germling cultures generally agree with the results recorded in stands of fucoid juveniles and adults (Creed 1995; Creed et al. 1998; Arenas and Fernández 2000). Thus, self-thinning in fucoid seaweeds appears to be as intense at the germling stage as at more developed stages.

Another density effect observed in terrestrial plants and seaweeds is the change in population size structure. In our study size, size inequality and skewness increased with settlement density in both *F. serratus* and *F. evanescens*, likely as a consequence of increased intraspecific competition. Size inequalities and positively skewed size distributions have been reported commonly for dense seaweed stands (Dean et al. 1989; Reed 1990; Creed et al. 1996a, 1996b, 1997, 1998; Arenas and Fernández 2000; Arenas et al. 2002; Karez 2003). The development of size inequality and positive skewness in seaweed populations is commonly attributed to dominance and suppression, where size distribution changes as competition becomes asymmetric and a few large individuals gain dominance and suppress many small ones (Creed et al. 1998; Arenas and Fernández 2000). If suppression is severe, it can lead to a proportionally higher mortality of small individuals and, as a result, re-normalise the population size structure (Weiner and Thomas 1986; Schmitt et al. 1987). This last phenomenon was not observed in our experiment, where even the highest crowding-induced mortality recorded (in high-density, nutrient-enriched *F. serratus* cultures at 17°C) failed to re-normalise the size distribution, possibly as a result of the limited time frame of the experiment. While previous studies have shown that size inequality lessens when nutrients become limiting (Weiner 1985; Creed et al. 1997) and natural variation in individual growth rates becomes less expressed (Turner and Rabinowitz 1983), nutrient enrichment stimulated mean germling growth without increasing size inequality in most treatments in our study.

Since the early 1900s, *F. evanescens* became increasingly abundant in the eutrophic inner Oslofjord area of southern Norway, while other fucoids (including *F. serratus*) declined (Grenager 1957; Bokn and Lein 1978). Following recent reductions in nutrient discharges, this trend appears to have reversed (Bokn et al. 1992). The exact mechanism behind these apparent nutrient-related changes in species abundance remains unknown, but interspecific differences in responses to nutrient enrichment at the germling stage might contribute. One contributing factor could be that growth and survival of germlings is more positively related to nutrient concentration in *F. evanescens* than in *F. serratus*. In our study, the growth of *F. evanescens* germlings was stimulated by nutrient enrichment at all density levels, whereas growth of *F. serratus* germlings was stimulated by nutrient enrichment only at the two highest densities, where competition for nutrients likely was more intense. In addition, the interspecific differences in self-thinning patterns suggest that the intraspecific competition ability of germlings is more positively related to nutrient concentration in *F. evanescens* than in *F. serratus*.

On the other hand, germling survival was independent of nutrient concentration and temperature in *F. evanescens*, but negatively related to nutrient concentration and temperature at the high settlement density in *F. serratus*. The reduced survival of *F. serratus* germlings under high-density, nutrient-enriched conditions at 17°C was possibly caused by a higher degree of crowding, as *F. serratus* germlings grew larger than those of *F. evanescens* in this treatment. Thus, for *F. evanescens*, population biomass comprises many small individuals, while approximately the same amount of biomass is tied up in fewer but larger individuals for

*F. serratus*. From an ecological viewpoint, it will be interesting to examine which of these two strategies in the end has the best odds for recruitment success. Competitive dominance is generally believed to be positively related to plant size (Grime 1977; Schmitt et al. 1986), so the larger *F. serratus* germlings may have a competitive advantage over the smaller *F. evanescens* germlings through shading effects. Precise knowledge on interspecific competition and on how it is modified by environmental variables, however, requires further experimentation. In mixed-species stands, both intra- and interspecific competition will likely co-occur; knowledge of intraspecific competition, as provided by our study, may serve as a baseline against which interspecific competition is calibrated (Paine 1990). Although the ecological, larger-scale implications of results recorded in short-term laboratory experiments are difficult to predict, our results suggest that growth and survival can be regulated by density during the early stages of substrate colonisation. Furthermore our results demonstrated that intraspecific competition effects on fucoid germlings depend on growing conditions (including settlement density, temperature, and nutrient levels) and species.

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